植物分類学報
4卷 2—4期 1955年10月

馬先蒿屬的一个新系統（上）

鍾補求
(中國科学院植物研究所)

序

在1948年夏，我開始研究馬先蒿屬，当時並未注意到李惠林氏在美國費城自然科学研究院正在作修訂本屬所有的中國种類的工作。当他的修訂的第一部分引起我的注意時，再來停止我在本屬中的工作，已覺太晚了，因为那時工作進度已深，幾已將英國邱園所藏的中國材料全部看完。他对於本屬進化的观點，確实給了我不少啓發，然而我对於他的系統排列方法，却仍然感覺不太滿意。此後我就很深入地來設法分析本屬中錯綜的親緣關係。为了这，我先从將研究範圍擴大到包括全世界的种類一點上着手，因为我很清楚，如果將研究局限於某一特殊地區，对於这方面是不会得到完整結果的。

在我对於本屬中系統的基本观念形成之後，我再參閱愛丁堡皇家植物園标本室、英國博物舘(自然歷史)植物部、和巴黎自然歷史博物舘等处所藏标本，來增加我对於本屬的知識。其後於1950年攜稿返國，想要在最短期內將它整理就緒。但为其他任务所拘，包括我二十个月的西藏之行，將这一方面的工作，遲延下來。一直到今夏才有工夫複看一遍，做了一些必要的修改和增訂，安排了揷圖及圖版，这个工作始成为可以付印的形式。

現在此篇已將付梓，我願借此机会向國外給我以方便的各机關的負責人道謝。

在回國之後，我曾受到本所所長錢崇澍教授的对於我所參加的每一工作的經常的、親切的關注，而且对於本文的發表，不但常常給与鼓勵，而且更承其檢閱原稿，我謹在此致以由衷的感謝。对於林鎔、張肇騫、吳徵鎰和姜紀五各位副所長的經常的、不倦的指導，亦就此謹表謝意。

我的先父鍾观光教授，很久以前就訓我繼承他的植物学研究。在1937年7月5日，我被調赴陝西武功中國西北植物調查所工作。兩天後，7月7日，日本軍國主义者在北京開始了他們的侵略战爭，他被迫回到出生地浙江寧波，不幸，三年後他因肺炎而去世了。在十七載以前，当我和他在北京分别的時候，再也夢想不到那是最後一次的訣别。在这裏，我願將这一个小小的工作，謹敬地献給永远親愛地留存在我的記憶中的他！

第一部 研究歷史

本屬在从前已經經过了多次的研究和修訂。各系統中比較重要的有1823年史帶芬

氏[1]的,1841[2]、1846[3]和1849[4]年彭奇氏的,1848年本生氏[5]的,1888年麥克齐姆維氏[6]的,1890年泊蘭氏[7]的,1910[8]与1918[9]年麗納蒂氏的和1924年林泊利許[10]氏的論著。經过了20年的沉寂,又同時分別各自地發表了兩篇著作,一篇是由古澤潔夫[11]寫的,另一篇是李惠林[12]所著。到了1949年底,那兩篇著作都已完成而可供研究了。

这些比較早的系統,虽然在李氏最近的修訂中,已把牠們的提綱列入討論中,可是一方面为避免查对就可以互相比較起見,另一方面也有因本人和李氏見解不同而感到他所引述的有不足之处,須加補充,所以在此再行補叙一次。

1. 史蒂芬氏系統

第一族:*Personatae*: 葉对生或互生;下唇直立。

第二族:*Verticillatae*: 葉四枚輪生;下唇伸展。

第三族:*Faucidentes*: 葉互生;下唇伸展,盔基部有齒。

第四族:*Rostratae*: 葉互生;下唇伸展,盔有喙。

第五族:*Bicuspidatae*: 葉互生;下唇伸展,盔端有二齒。

第六族:*Edentulae*: 葉互生;下唇伸展,盔端無齒。

在上面的系統中,有一點極为有趣,这就是將所有具有直立下唇的种類孤立起來,另立一族,名为 *Personatae*, 以与所有其他具有伸展下唇的种類相对立。这种措施,是在比較後來的許多著者的工作中所不見的。正与麗納蒂氏的評語"他的出發點是不自然的"这种意見相反,这一點,事实上是在本屬分類中最重要的特徵;这表示著者对於本屬中存在着兩种根本不同的花冠型式的事实,有所重視。这种型式,可以称之为"基本花冠型式",如不將它區別出來,將使一个眞正的自然系統的实現,成为不可能,其理由何在,尙待以下詳論。

但是他的系統,由於缺乏对这兩种"基本花冠型式"相互關係的澈底瞭解,也是不能使人完全

1) Steven, C.: Monographia Pedicularis, in Mém. Soc. Nat. Moscou, VI, i(1823),60,pls. 1-17.

2) Bunge, A.: Ueber eine neue Art der Gattung Pedicularis, in Bull. Acad. St. Pétersb., VIII (1841), 241-253.

3) Bunge, A.: Ueber Pedicularis comosa L. und die mit ihr verwandten Arten, in Bull. Phys.-Math. Acad. St. Pétersb., I(1846), 369-384.

4) Bunge, A.: Pedicularis, in Ledebour, Flora Ross. III(1849), 268-303.

5) Bentham, G.: Scrophulariaceae, in DC. Prodr. Syst. Nat. Regni Veget. X(1846), Pedicularis, 560-582.

6) Maximowicz, C. J.: Pedicularis L., Synopsis generis nova, in Bull. Acad. St. Pétersb. XXXII(1888), 515-619, pls. 1-7, et in Mél. Biol. Acad. St. Pétersb. XII(1888), 769-919, pls. 1-7.

7) Prain, D.: The species of Pedicularis of the Indian Empire and its frontiers, in Ann. Bot. Gard. Calc. III(1890), 1-196, pls. 1-37, 1 map.

8) Bonati, G.: Contribution à l'étude du genre Pèdicularis, in Bull. Soc. Bot. France, LVII (1910), Mém. 18, 1-35.

9) Bonati, G.: Le genre Pedicularis L. Morphologie, classification, distribution géographique, évolution et hybridation (1918), i-x, 1-168, 1 pl.

10) Limpricht, W.: Studien über die Gattung Pedicularis, in Fedde, Rep. Sp. Nov., XX(1924), 161—265, 1 map.

11) Hurusawa, S.: The genus Pedicularis, in Journ. Jap. Bot. XXI(1947), 159-166, XXII (1948), 11-16, 70-76, 178-184, XXIII(1949), 20-24, 106-112.

12) Li, H. L.: A Revision of the genus Pedicularis in China, pts. I & II, in Proc. Acad. Nat. Sci. Philad. C(1948), 205-378, pls.15-23, et CI(1949), 1-214, pls.1-16.

滿意的。这是表現在將有些具有明顯的 "Personatae" 式花冠構造的种類，像 *P. tristis* L., *P. acaulis* Wulf 等等，放在 *Personatae* 族的外面。

除了將輪生葉的种類自成独立的一族外，他的系統中的大部分，自第三至第六族，已經大大地受了全由進化後果而來的花冠發展型式的压倒一切的影响了；这种發展型式，因为用对比的方法，易於得到較为清晰的印象，所以可以將它称为"進化花冠型式"，以与上面所称的"基本花冠型式"相对立。他的所以未能在这兩种对立的"基本型式"的各自的範圍內，追尋它們的進化路線的緣故，也許是由於他所知道的种類太少，所以不能像現在我們所有的丰富的材料一般，足以没有間断地表示出这种親系的關係來。这样，他的系統，在意义上說來已經是人为勝过自然了。

2. 彭奇氏系統

彭奇氏共組織了三套系統。其第一套在 1841 年發表，如下：

Verticillatae: 葉輪生或对生。

第一組：*Erostres*: 盔無嘴。

第二組：*Rostratae*: 盔有嘴。

Sparsifoliae: 葉互生，極少对生。

第三組：*Tubiflorae*: 花具長管。

第四組：*Rostratae*: 盔有嘴。

第五組：*Platyphyllae*: 寬葉。

第六組：*Basidentatae*: 盔基部有兩齒。

第七組：*Bidentatae*: 盔端有兩齒。

第八組：*Edentatae*: 盔無齒。

第九組：*Macrantha*: 花大，下唇直立。

这一系統在將 *Verticillatae* 独立上是与史蒂芬氏相同的。在互生葉的領域裏，系統的性質似乎更为混雜。第九組 *Macrantha* 分明部分地等於史氏的 *Personatae*，但是把 *P. tristis* L., *P. capitata* Steven, 与 *P. acaulis* Wulf 包括在內，很明顯地表示了他对於"基本花冠型式"的進一步的瞭解。另一特點是在創造一个与花冠無涉的組，*Platyphyllae*，裏面包含着一些种類像 *P. resupinata* L., *P. lanceolata* Michx., *P. bifida* Pennell (*P. carnosa* Wall.), *P. racemosa* Douglas 等等，都具有很相類似的形态。虽然其他各組，还是以"進化型式"为依据，但在較早的系統中，是很合理地可以称为較好的一个。

也許因为在第二和第四組中，*Rostratae* 的重現的關係，也許另有緣故，他在 1846 年又把他的系統重排如下：——

第一組：*Cyclophyllum*: 葉輪生或对生。

第二組：*Siphonantha*: 葉互生，花有長管。

第三組：*Rhyncholophae* 葉互生，花有長嘴。

第四組：*Pharyngodon*: 葉互生，盔近喉处有二齒。

第五組：*Lophodon*: 葉互生，盔近端处有二齒。

第六組：*Anodon*: 葉互生，盔無齒。

第七組：*Macrantha*: 葉互生，下唇直立。

在这裏所有輪葉的种類是被簡單地集合在 *Cyclophyllum* 組內；也有許多新的名称被介紹給一些組。*Platyphyllae* 組則被略去，而它的种類，都被放入 *Rhyncholophae* 組內。

三年以後，另一含有某些改变的系統出現如下：

甲. *Pedicularis-legitimae* 亞屬：下唇伸展或伸直，不包裹盔部。

第一組：*Cyclophyllum*.

第二組：*Siphonantha*.

第三組：*Rhyncholophae*.

第四組：*Pharyngodon*.

第五組：*Lophiodon*.

第六組：*Anodon*.

甲甲. *Sceptrum* 亞屬：下唇包裹盔部，葯室鈍头。

甲甲甲. *Diacmandra* 亞屬：下唇包裹盔部，葯室有長尖。

在这裹，下唇的長短与它和盔部的对比，前者是否包裹後者这一點是特别地被强調了。这一點配合着雄蕊葯室的形狀，供給为分亞屬的特徵。这在事实上說來是还不如他以前的一个系統，值得称許，因为下唇的長短，並不如它的位置的伸展或直立为重要；为了这點的过份强調，*P. Sceptrum-carolinum* L.、与 *P. grandiflora* Fisch. 就与和它倆極近的 *P. capitata* Adams、*P. acaulis* Wulf 和 *P. tristis* L. 相离異了，因为这三种所屬的 *Macranthae* 系是被放在 "*Pedicularis-legitimae*" 亞屬下的 "Anodon" 組中的。还有，照現在我們所知的，具有凸尖的葯室，也在 *P. centranthera* Gray, *P. plicata* Franch., *P. pycnantha* Boiss. 和 *Aloenses* 系中的大部种類中發現，所以不值得这样重視，以为具有亞屬的重要性。

3. 本生氏系統

第一系：*Verticillatae*: 葉輪生。

1. *Longirostres*: 花有長嘴。
2. *Brevirostres*: 花具短嘴。
3. *Erostres*; 花無嘴。

第二系：*Siphonanthae*: 花具長管，葉互生(以下同此)

1. *Longirostres*: 花具長嘴。
2. *Erostres*: 花無嘴。

第三系：*Faucidentes*: 花喉有齒。

1. *Longirostres*: 花具長嘴。
2. *Brevirostres* (vel Erostres)：花具短嘴(或無嘴)。

第四系：*Bicuspidatae*: 嘴端具双齒。

1. *Ramosae*: 莖分枝。
2. *Gladiatae*: 莖簡單；葉單羽狀分裂。
3. *Comosae*: 莖簡單；葉分裂較多。

第五系：*Edentulae*: 花不具齒。

1. *Foliosae*: 莖葉發達；花穗長，盔無嘴。
2. *Uncinatae*: 莖高昇，有葉；花穗長，盔有嘴。
3. *Scapiformes*: 莖作花莛狀，少葉或無葉；花穗短，盔有嘴，無毛。
4. *Humiles*: 莖多变化，低矮；花穗短而密，盔無嘴。
5. *Tristes*: 莖高昇，盔無嘴或具短嘴，緣有長毛。

6. *Racemosae*: 莖分枝，葉有細圓齒或偶而細裂；花總狀，盔有嘴，偶而無嘴。

7. *Acaules*: 莖不發育。

第六系：*Personatae*

这些較高的他所称为"系"的分類階層，分明等於史蒂芬氏的"族"，所不同的只是他把具有長管的种類另立为一羣，名为 *Siphonanthae*." 在較低的，眞眞等於系的階層中，所选用的特徵，更比本奇氏为無恆，这可以在前面三系的完全以花部特徵为主，而在第四、五系中則又矛盾地以营养器官为主的事实上看出來，这表示出在自然的与人为的兩种系統排列中的未得定論的競爭。正如泊蘭氏所指出的(第一頁)一样，这个系統的眞正價值，是在於開始將相近的种類，聚合为系，而这些系在他以後成为所有系統的基層組織。

4. 麥克齐姆維氏系統[1]

第一族：*Longirostres*：花管圓筒形，雄蕊着生於管頂，嘴一般都長。

1. *Siphonanthae*：葉互生。

2. *Longirostres-verticillatae*：葉輪生。

第二族：*Rhyncholophae*：花管圓筒形，近喉处膨大，盔多少具長嘴，少有無嘴，前緣無齒；葉互生。

第三族：*Verticillatae*：花冠多变，决無長嘴；葉对生或輪生。

第四族：*Bidentatae*：盔具幾不發育的嘴或無嘴，前緣近端处有兩齒；葉互生。

第五族：*Anodontae*：盔無嘴，边全緣，額部圓；葉互生。

除了自本生氏留下了 *Verticillatae* 之外，麥氏的系統，更深陷入於完全人为的安排中，因为在这裏，被本奇氏及其他以前的著者所重視的"基本花冠型式"的对比，第一次被完全拋棄。其眞正的價值，則在於將本生氏所始創的各系，加以推廣，使更为具体，和他对於所有种類的親切的認識，而且多附有在本屬研究中所僅見的最精緻的圖解的幾點上。

5. 泊蘭氏系統。

第一部：*Longirostres*：花管直而細，上下一律；唇片大，無柄，質地較堅厚而比有長嘴的盔部为柔薄。

第一組：*Siphonanthae*：花管很伸長；雄蕊着生於管的中部以上；葉互生。

第二組：*Orthorhynchae*：花管較短；雄蕊着生於花管近基处；葉輪生。

第二部：*Aduncae*：花管彎曲，圓筒形，在近喉处稍稍膨大；唇無柄或有柄，比有嘴或無嘴的盔部为柔薄。

第三組：*Rhyncholophae*：盔有嘴，有時無嘴。

第四組：*Bidentatae*：盔無嘴或有短闊的嘴，端下有兩齒。

第三部：*Erostres*：花管內曲，漏斗狀；唇有柄，基部直立，上面有二喉脊，伸張，与無嘴的盔部同質。

第五組：*Anodontae*：盔直立，無嘴或有原始的短嘴，無齒或僅在緣的下部有齒，頂端圓形。

在上面的系統中，我們看到了他对於花冠的观察其精密程度远过於从前著者。但是他的缺點，是因为失於將"基本型式"从"進化型式"分別開來，所以將这兩組完全不同的型式混合起來，

1) 他的第一个系統，發表在 Mél. Biol. X (1877) 和 Bull. Acad. Sci. St. Pétersb. XXIV (1877) 裏面，並不和第二个 1888 年發表的有很大出入，所以省略未予論及。

以致卓越的努力多少成为浪費。很明顯地，在这裏是無法詳論各點的，但是我們不妨指出一兩點來，作为我們批評的意見。拿花管和雄蕊着生點的關係來做例子吧。在短管的种類中，雄蕊向例是着生在管的基部的，正像在長管的种類中，其着生點是常常接近管的喉部；这很明白地表示出这一特性，是進化性的。但是照我們在有柄的下唇这一特徵看來，这是与"基本花冠型式"的區別，保持着密切的联繫的，因为这僅在兩种"基本型式"中的一种裏看得到，而在另一种裏是完全不可能看到的，所以这是可称为本質的（不是後生的）特徵。以後对於这些还要詳論。至於这个系統，虽然花了不少功夫，在系統的性質上來講，可以說並沒有多少貢献。当然，像麥氏一样，他对於各系的明確的观念和对它們的大大改進，以及他对喜馬拉雅种類的精確的認識，是無可批評的。

6. 麗納蒂氏系統(1910)[1]

第一部：*Erostres*：盔無嘴。

第一族：*Anodontae*：盔無齒。

第一組：*Anodontae-alternifoliae*：葉互生。

第二組：*Anodontae-verticillatae*：葉輪生。

第二部：*Rostratae*：盔有嘴。

第二族：*Bidentatae*：花冠之管多向喉部擴大，盔端下有双齒。

第三組：*Bidentatae-alternifoliae*：葉互生。

第四組：*Bidentatae-verticillatae*：葉对生或輪生。

第三族：*Rhyncholophae*：花冠之管向喉部擴大，盔全緣。

第五組：*Rhyncholophae-alternifoliae*：葉互生。

第六組：*Rhyncholophae-verticillatae*：葉对生或輪生。

第四族：*Longirostres*：花冠之管圓筒形，上部不膨大，盔全緣。

第七組：*Siphonanthae*：葉互生。

第八組：*Orthorhynchae*：葉輪生或对生。

他虽然引入了許多的变更到系統中來，但其基本的观念並沒有受到任何劇烈的改易，因而他的系統还是和泊蘭氏的差不多。在他对於歐洲產的馬先蒿作了廣泛的雜交研究之後，一个新的观念引導他到一个不準確的、但却是很有趣味的結論上去，这个結論即作为他的第二个系統的基礎。这个观念[2] 就是認为"*Anodontae*"（無齒系）与"*Bidentatae*"（双齒系）是从同一个祖先即假設的"*Paleo-Pedicularis*"（太古馬先蒿）中出生的，而不是一个从另一个中演化而來，所以是具有同等的地位。这一个 *Paleo-Pedicularis*（代以 X）最先發展为兩羣，一羣是 *Paleo-Erostres-Alternifoliae*（古無齒互葉羣，代以 X^1），另一羣是 *Paleo-Erostres-Verticillatae*（古無齒輪葉羣，代以 X^2）。从 (X^1) 中再發生兩羣 *Bidentatae-alternifoliae*（双齒互葉羣，代以 CP）和 *Anodontae-alternifoliae*（無齒互葉羣，代以 $C'P'$）。从 (X^2) 裏生長出 *Bidentatae-verticillatae*（双齒輪葉羣，代以 $C'_1P'_1$）和 *Anodontae-verticillatae*（無齒輪葉羣，代以 C_1P_1）。因为缺少与他羣中發生雜交情形，所以互生葉的和对生葉的"双齒羣"都被認为在親緣上与較高

1) 李惠林錄出了麗氏的一个系統，他以为是 1918 年的，但其实是 1910 年的而由麗氏自已再以更確定的方式，在 1918 年重行發表；他的新系統放在後來發表的这一著作中的最後部分（第 157 頁）是完全地被李氏所忽視了！

2) 請檢閱麗氏的面对着 158 頁的第十表格。

的各羣比較疏远，而它們的進化活動都在它們各自原來的位置上停頓住了。花部進化的作用，應断是單單由互生葉和輪生葉的 *Anodontae*(無齒羣)繼續，而經由 *Rhyncholophae-alternifoliae* (喙盔互葉羣) 和 *Hypothorhynchae* (弱喙羣)分别到達高度專化的 *Siphonanthae* (管花羣) 和 *Orthorhynchae* (直喙羣)。由此而來的是他的1918年的系統：

第一部：*Bidentatae*.

第一組：*Bidentatae-alternifoliae*

第二組：*Bidentatae-verticillatae*

第二部：*Edentatae*

第三組：*Anodontae-alternifoliae*
第四組：*Rhyncholophae-alternifoliae*
第五組：*Siphonanthae*
} 葉互生。

第六組：*Anodontae-verticillatae*
第七組：*Hypothorhynchae*
第八組：*Orthorhynchae*
} 葉对生。

在得到这样一个結論時，他却漠視了一个十分嚴重的衝突點。在159頁中，他自己分明曾經談到在困人的 *Superbae* 系中，*P. superba* Franch. 是屬於 *Hypothorhynchae* 而 *P. cyathophylla* Franch. 屬於 *Orthorhynchae*。在1910年，以具有双齒的 *P. rex* C. B. Clarke 作为依据，把这一系放在 *Bidentatae-verticillatae* 中，而在1918年，他分明也还是没有更变它的位置的意思。旣承認 *P. superba* 为一种 *Hypothorhynchae* 与 *P. cyathophylla* 係一 *Orthorhynchae* 而同時又把它們一起放在 *Bidentatae-verticillatae* 裏面，他不但把自己的 *Bidentatae* 停止進化的假說否定了，而且也嚴重地攪乱他的系統的和諧性。

由上述一羣(最廣义的 *Superbae* 系)他更申說到互生和对生葉的种類，是隸屬於兩个並行發生而独立的羣的。这明顯地是与李氏的想法相同而也是李氏的先驅者。虽然如此，他还是拿葉序來作次一級分類的基礎，而並無所更張。

7. 林泊利許氏系統。

甲. *Erostres*.

1. *Anodontae-alternifoliae*
2. *Anodontae-verticillatae*
3. *Bidentatae-alternifoliae*
4. *Bidentatae-verticillatae*

乙. *Rhynchophorae*.

5. *Rhyncholophae-alternifoliae*.
6. *Rhyncholophae-verticillatae*
7. *Longirostres-siphonanthae*
8. *Longirostres-orthorhynchae*

林氏的系統主要还是和麗氏1910年的相同，不过更整齐地按照"進化型式"排列而已。虽然在文末的親緣表中，由於不將 *Salviaeflorae* 系列入 *Verticillatae*[1] (輪葉羣) 中而把它跟隨

1) 請参閱400頁後的親緣表1与2，和地理分佈圖。

着 *Gloriosae* 系之後，可以看出他的对於在兩种“基本型式”間的不同有所鑑别，但是这並未使他捨棄了以前著者的老路，而在他的系統中，終於把那一种仍放在 *Anodontae-verticillatae* 之中。

8. 古澤潔夫氏系統

古澤氏的系統(日文)以拉丁文作檢索表，將本屬分为兩个亞屬，十个組和很多的亞組。今將其表中的分羣，重新寫在下面，以表出他的大意來：——

甲. *Rhynchophorum* 亞屬：盔有嘴，僅在 *P. Perrottetii* Bth. 中無嘴。

第一組：*Siphonanthae*：葉互生。

Rhinanthoides 亞組。

Muscicolae 亞組。

第二組：*Orthorhynchae*：葉輪生。

第三組：*Tibeticae*：葉互生。

第四組：*Axillares*:：葉輪生或互生。

第五組：*Hypo-orthorhynchae*:：葉輪生。

第六組：*Rhyncholophae*:：葉互生。

乙. *Sceptrum* 亞屬：盔無嘴，全緣或有双齒。

第七組：*Hyporhyncholophae*：葉輪生。

Ikomanae 亞組。

Lyratae 亞組。

第八組：*Metanodontae*:：葉輪生。

Caucasicae 亞組。

Cyclophyllae 亞組。

Moschatae 亞組。

第九組：*Lophiodon*

Palustres 亞組：葉互生。

Comosae 亞組：葉互生。

Striatae 亞組：葉互生或对生。

第十組：*Anodon*：葉互生。

Acaules 亞組。

Grandiflorae 亞組。

Lanatae 亞組。

在上面，虽然將久已被捨棄了的本奇氏的 *Sceptrum* 再行介紹進來作为亞屬，但其命名人給它規定的原意，却已完全失去，因为我們可以看到在它下面排放着許多完全不同本質的羣，像具有伸展下唇的 *Lanatae, Moschatae* 和与它們远距而具有直立下唇的眞眞的 “*Sceptri*” 像 *Striatae, Acaules* 与 *Grandiflorae* 同列一处。即使是多多地更換了各階層的名称，古澤潔夫氏的系統实質上还是和林氏的無别，因为他的 *Rhynchophorum* 和 *Sceptrum* 完全与前一作者的 *Rhynchophorae* 和 *Erostres* 相等的。

在開始討論李惠林的建立於完全不同之基礎上的系統之前，我們可先將以上所述的系統，作一總結。这些大約可以分为兩類。第一類可認为混合系統，如像史蒂芬、彭奇、本生等氏者；第二

類是完全人为系統、像麥克齐姆維、泊蘭、麗納蒂、林泊利許和古澤潔夫等氏者。在第一類中，对於"基本花冠型式"的差別，是曾加以注意的，但是因为將这种差別，未能追蹤到進化得較高的領域內，所以只將比較原始的一些种類，來加以區別。而且这种區別，也並沒有加以标準化，所以區別開來的种類，也顯得零乱。在第二類中，就連这一方面的少許注意，也被完全地放棄了。这种大部或全部地以"進化花冠型式"为依据的系統，將同在一个進化階段之上，而在親緣方面很少關係的种類，都放在一个組中，因而無例外地使人產生一种"橫"的感覚，而这对於達成一个眞正的自然系統，成为嚴重的障碍。从各位作者的討論中可以看出，他們之中，尤其像林泊利許氏，並非对於較高的分類單位之間的親緣關係，全無理解，但是这一類系統的安排方法，簡直無法把親近的系，排放在一个直線的次序上去。在有些情况之下，某羣的花部構造和营养器官的特徵之間，因受到这种不合理的排列方法的影响，而發生出这样强烈的矛盾來，以致於在这种以"進化花冠型式"为基礎的系統中，任从給它以何种位置，都將無法取得协調。这也可以在 *Cyathophora* 羣中，得到活生生的例子。李惠林已經指出，这一羣实質上就等於那一个舊的，無所不包的 *Superbae* 系。这一羣內的种類，在营养器官上都有一个特徵，不可能与其他羣中的种類相混同，那就是結合为杯狀的葉基和苞片。另一方面，在它們花冠的構造上看來，少數的种類，却佔着四个不同的進化階段，从"*Bidentatae*"(双齒型)起，以達到"*Longirostres*"(長喙型)。这裏我們要感謝这种营养器官上的徵候，牠是这样地独特，以至於把这些种類，完全緊密地結合在一起而成为不可分割的一个整体。在这种情况下，如果犧牲了这一特徵而遷就原为系統基礎的花部構造，而將它們分放在四个依照它們各自花冠類型的組中，那是任何人都会感覚不合理的。反过來，如果依靠这一营养器官的特徵，而將它們勉强地放在一个系內，而再按照这个系內的三个花冠進化型式中的任何一个，而放它入於一个組內，那麼不用說都会知道，除了那被选中的一个花冠型式之外的其餘兩个型式，勢必發生無法消除的衝突，而使整个系統，失去它应有的和諧。所以如果系統的安排無所改变，那麼，那兩种方法之中，必須抉擇其一，虽然这兩者都是肯定地不合適的。在以上的著作中，差不多無例外地採取了後面一种办法。麗納蒂氏把它們都安置在"*Bidentatae*"裏面，虽然他在这样做時，分明感到不安，因为他的1918年的地理分佈的一節內，曾頗有歉意地說过"*P. superba* 这一种，是屬於 *Superbae* 系的，而这一系的排列是十分为难的。……(第63頁)。但是，在这特殊的营养器官与花冠構造之間所表出的衝突，却未曾給这一位著者以充份的啓示，使他感覚到自己的系統，是立足於完全錯誤的基礎之上，从而用一个澈底的修訂，來把这种衝突消除掉。同样地是林泊利許和古澤兩氏，他們也毫無更張地把这一羣(系)，分別安放在"*Bidentatae-verticillatae*"和"*Hyporhyncholophae*"之中。

李惠林氏系統

也許是由於安揷那个舊的，充滿矛盾的"*Superbae*"系時所引起的兩难情形，使李惠林理会到以前所有的系統，是建立在完全錯誤的观點上的。一种以为各式花冠如無齒、有齒、有嘴、以及長管等，僅僅是進化的後果，如果据以为系統的基礎，則勢必將進化的關係切斷的这样一个概念，得以形成，而一种革新的步驟，也从而被採取。替代了以"進化花冠型式"为主，他的着重點是被放在体态和葉序上面了。結果是，因为他的系統，正与以前的相反，所以可以說不再是完全"橫"的，而在某一程度上，已成为一个"直"的系統了。这样的一个多少直的次序，使得有可能創造較大的自然集羣(在他系統中的組)，在这裏面，將有着血統親緣的，但是正在不同進化階段上的种類，歸納到不同的系中，而後將这些系，按照進化的高低，系統地排列成組。來表明这一見解，我們还是引用那一个舊的"*Superbae*"系，亦即現在的 *Cyathophora* 羣(李氏的組，見 Revision

I, 257 頁), 來作例子, 比較更清楚些。在那舊系中的在四个不同進化階段中的种類, 依着它們的程度, 都被提昇起來以代表系, 而後按序排列成为 *Reges*、*Cyathophylloides*[1]、*Superbae* 和 *Cyathophyllae*, 以合成一个新的 *Cyathophora* 羣 (組)。这似乎再也找不出一种比这更能闡明親緣關係的方法了。但是, 分明由於他对於形态的研究, 尙嫌不足, 至使被 *Cyathophora* 羣中的强有力的証据所說服, 而發生了与麗納蒂氏相同的观念。他和麗氏都認为所有輪生葉的种類, 在進化上是屬於完全独立的一个分枝的; 在这样的观念下, 当然將互葉羣和輪葉羣之間的营养器官和花部構造的相似點, 都籠統地、武断地歸納到並行進化的这一个原因中去。这样地以葉序为主要分野, 就將本屬分为三个大羣如下:

第一羣: *Cyclophyllum* 輪葉羣, 葉对生或輪生。

第二羣: *Allophyllum* 異葉羣, 葉互生或对生, 或兩全。

第三羣: *Poecilophyllum* 变葉羣, 葉性狀同上。

拿葉序來做系統基礎, 是一个頗有疑問的方法, 因为这样做同样地也給系統帶來了某种"橫"的感覚, 虽然这是与"進化花冠型式"为主的系統所具有的"橫"的感覚大大地有所不同, 然而还是不免其为"橫", 因为这种系統把許多極相親近的种類, 安置到相距極远的分類位置中去。再者, 我也覚得难於同意这位作者的以全部輪生种類为原始的一种概念。对於这些問題, 我們以後当然还要詳加討論, 而这样複雜的問題, 是無法在这裏加以闡明的。这些使他的系統大大減色的缺點, 無疑地是由於像許多晚近的作者一般地沒有能够分辨"基本花冠型式"的區別的緣故, 而这些缺點, 是充份地表示在他的親緣表中似乎很少主宰地排放着各組各系的情形中的。

虽然李氏沒有能把帮助他將有些重要的羣 (組) 像 "*Lasioglossa* 和 *Rhizophyllum* 等串合起來的形态特徵, 以具体的方式講出來, 但是他的系統是比以前的大大地前進了一步, 而为所有系統中最自然的一个, 却是毫無疑問的!

二. 形态与進化

(一) 在進化观點下作为系統基礎的主要及其他形态特徵

在以前馬先蒿屬的專著中, 各种形态的特徵, 幾乎無例外地, 是不被看作具有內在相互作用的有机整体的一部分, 因而应該在進化的观點上把它們联合起來研究的, 而是把它們看成孤立的項目而可以用表格的方式來条陳。由於这种支离脫節的方法, 除了被当作系統基礎的特徵以外, 其餘的只个別地拿來區別种類, 而一律被擯棄在系統思考之外了。但是, 十分明顯, 祇有把所有的特徵都融会到系統中去, 才有希望成为既完备而又合理的安排。因为方法的不同, 我們的論述, 將不按自根部到种子的慣例, 而將以各种特徵的重要性为其先後的次序。

1. 兩个"基本花冠型式"和它們在發生中的根本區別。

一如李氏所指出, 本屬植物的受精作用, 主要恃昆虫授粉, 所以花冠的構造就被採取为对

---

1) 李氏在他的修訂論文中 (Revision I, 334—335), 把 *Cyathophylloides* 系, 放在 *Reges* 系之前, 而作为 *Cyathophora* 組的開端, 是很不合理的。这一个單一的模式种, 已經具有膨大而略具嘴形的盔部, 和相当伸展的下唇 (虽然在他的圖中, 下唇是被画得过份地伸張了), 而 *Reges* 的盔, 是双齒型的, 而唇部相当掩合, 前者比後者進化, 是毫無疑問的。

於这一方面增加效力的步驟。这些進化較高的种類，可能各自適应於一种特殊的昆虫[1]，在純形态学观點上看來，是極饒趣味的，但是無疑地缺乏分類学上的價值，因为不但它們的花冠，已經从原來型式改变得太多而使人難於辨認，而且它們的营养器官也在進化过程中有了或多或少的变化。实在說來，在一个真正的自然系統中，这些花冠進步的構造，是不应該使用到比系更高的階層中去。所以一个分類学家的正確方法是在比較原始的种類中找到主要的區劃特徵，而後以各种形态特色为輔助，來追求進化的趨势，才可以得到屬中較高區分的概念。

当研究以前所有的系統時，我曾深被較早的作家們对於某种特殊型式的花冠格外注意的事实所影响，这种花冠就曾使史蒂芬与本生兩氏立出 *Personatae*，彭奇氏創立 *Macranthae*，*Sceptrum* 和 *Diacmandra* 等"族"和亚屬來，以与他們各自的系統中其他一种型式相对立。更拿以上观點，來与後來各作家的思想如泊蘭氏对於下唇形狀的區別（第八頁），釐納蒂氏对於盔上齒的發生[2]，和李氏的对於管部的弯曲[3] 等等相联繫起來，就開始形成了一种与"進化花冠型式"無關而完全独立的"基本花冠型式"的一个確定观念。

虽然它們之間的对照，也許不如在"進化型式"中所見的强烈，然而这兩种"基本型式"在構造上是这样地有區別，因而在比較原始一些的种類裏面，即使是在乾燥的标本中，也是極易辨認的。拿兩組标本來做例子吧，一組是：*P. capitata* Adams、*P. Sceptrum-carolinum* L.、*P. salviaeflora* Franch. 和 *P. rex* C. B. Clarke；另一組是：*P. Oederi* Vahl、*P. foliosa* L.、*P. abrotanifolia* M. Bieb. 和 *P. pilostachya* Maxim.，这兩組中都含有互生葉和对生葉的种類各兩种。每个有經驗的工作者，决不会看不出在第一組中的四种具有伸直的管部，直立的唇部，而第二組中的管部，則在近端处突然向前俯曲，而下唇与管部和盔部的關係則是多少以直角伸張。这些區別是曾經引起早期著者的注意过的。为了便利計，第一种將被名为"*Capitata* 型"而第二种为"*Flammea* 型"。

以上所述不过是这兩种"基本花冠型式"粗放的定义。在細緻地考察了各部花冠構造之後，將会發現足以加强这裏所提議的兩种"基本型式"之可靠性的其他重要特徵。花冠的各部，將分別詳論。为了利於討論，必須先提及行將具体地代表此兩种"型式"的兩羣植物。在 *Sceptrum*[4] 羣中的 *Eusceptrum* 亚羣，裏面大略包括 *Tristes* 系（狭义）、*Dolichocymbae* 系、*Ingentes* 系、*Lasiophrydes* 系、*Trichoglossae* 系、*Kongboenses* 系和 *Subsurrectae* 等系，將代表"*Capitata* 型"，而 *Rhizophyllum* 羣中的 *Eurhizophyllum* 亚羣，約含 *Flammeae* 系、*Pseudo-Oederianae* 系、*Rhynchodontae* 系、*Filiculae* 系、*Robustae* 系、*Macrorhynchae* 系、*Longiflorae* 系和 *Megalanthae* 系等，將用來代表"*Flammea* 型"。此第一个羣只不过等於以前著者所意象的最廣义的 *Tristes* 系，而第二个羣也只是与李氏的 *Rhizophyllum* 組相同而稍稍加入幾系而已。凡对本屬有相当熟悉的人，是很容易辨識在此兩羣中的，尤其在其基層中的，毋容爭辨的那种親緣連續性的。

下面是对於花冠各部的論述：

---

1) 很奇異地，在我的西藏旅居和行程的二十个月中，我僅僅得到兩次机会，看到了土蜂拜訪了兩种馬先蒿，一种是 *P. lachnoglossa* Hk. f. 另一种是 *P. globifera* Hk. f. 在这兩次中，土蜂並沒有採取花蜜，却是忙於收集花粉。如果誰能在適当的季節裏，有机会逗留在富有馬先蒿种類及个体的地方，來观察昆虫的活動。这無疑地將会是一个極饒兴趣的研究。

2) 对照在 82 頁中所引釐氏言論。

3) 对照李氏書第二部 300 頁中 *Verticillatae* 系中的論述。

4) 在討論各羣和亚羣時，請讀者参閱文末的親緣表。

(1) 盔部——在盔部中，当然以在很多种類中發生的齒为最重要了。在与其他形态特點联繫起來而仔細地研究这种特徵中的各种型式之後，我們就尋着了它的根源，这就更增加了我对於"基本型式"的信心。在一种型式中的完全缺如，和表現在另一种型式中的顯明的發育階段，是不容漠視的。

現在讓我們來細細地考察一下在上述兩羣中的盔部進化情形吧。在 *Eusceptrum* 亞羣中有一件事曾引起麗納蒂氏注意的就是从"無齒型"直接進化到"有喙型"，而中間並不經过"具齒"的階段。在第 97 頁(1918)，他是这样表示意見的：

"無齒羣"相反地是生出"有喙羣"來的，而且这並不是一种假設而是事实；只要檢視一下有些自然的系，像 *Resupinehs* 和 *Tristes*，就足以使人置信了；我們可以証明，尤其是在後面一系中存在着許多中間的型式，从盔部無嘴而前面閉合如 *P. tristis* L. 經由一些种類具有舟狀的盔部如 *P. Prainiana* Maxim., *P. princeps* Bur. et Franch. 而達於具有長嘴的 *P. ingens* Maxim., *P. lasiophrys* Maxim., 等……"。

他的說法和他所举來解釋他的看法的兩个系，*Resupinatae* 和 *Tristes*，都只是部分地和事实相符，因为这顯然不是一个普遍的規律，凡是"有喙型"（*Rhyncholophae*）都是从"無齒型"（*Anodontae*）直接進化來的，事实上我們現在已有充份的証据，知道 *Resupinatae* 系是由全部均具有双齒的种類所組成的 *Palustres* 系進化而成。但是講到 *Tristes* 系，那麼他的看法是準確的。要把这个观點更具体地表示出來，最好的方法，是把在那一羣中处在不同發展階段的各种花冠類型，並列在一起。从具有無嘴的盔部的 *P. tristis* L. var. *macrantha* Maxim.（圖 1, A），進入到 *P. dolichocymba* H.-M.（圖 1, B）的具有虽短而却明顯的嘴部的階段，然後繼續發展成为長嘴的种類如 *P. trichoglossa* Hk. f.（圖 1, C）和 *P. Vialii* Franch.（圖 1, D）等。在这种發展的生嘴过程中，顯然地是並未牽涉到有齒的階段的。

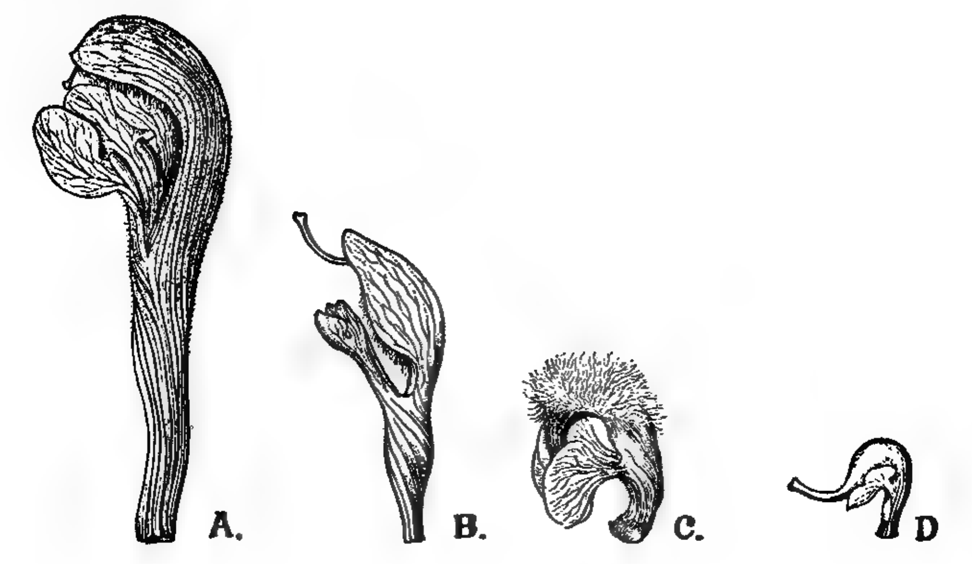


圖 1. A. *P. tristis* L. var. *macrantha* Max.; B. *P. dolichocymba* H.-M.; C. *P. trichoglossa* Hk. f.; D. *P. Vialii* Franch. × 1½

与上述的形成生動对比而同時又係 *Eurhizophyllum* 亞羣中最明顯的特徵之一，那就是不同階段的具齒的盔部。在 *P. Oederi* Vahl (圖 2, A) 中，盔部的形狀，幾乎没有和 *P. tristis* Linn. 很不同的地方。在第二階段，一个前端有稜角的盔部出現在 *P. pseudoversicolor* H.-M. 中，这無疑地是在 *P. habachanensis* Bonati (圖 2, B) 中所發生的一个眞正具有双齒的盔部的前奏曲。但是最有意味的步驟，却在 *P. rhychodonta* Franch. (圖 2, C) 中，那裏除了存在着一对主要的齒以外，在已經多少伸長成嘴的頂端，还增加了幾个附屬的較小的齒。在下一階段的 *P. filicula* Franch. (圖 2, D) 中，嘴部的伸長，虽又向前推進了一步，而嘴端的齒，則已处於抑制狀态之下，主要的一对已經消失而附屬的小齒則猶然存在，所以嘴端形成嚙痕狀。在以後的階段中，如 *P. Wallichii* Hk. f. (圖 2, E) *P. robusta* Hk. f. 等种，这些种類多顯示其有齒的特徵於强二裂的嘴部，而此特徵幾成为此亞羣中較高程度的各系的标誌，这可以 *P. Klotzschii*

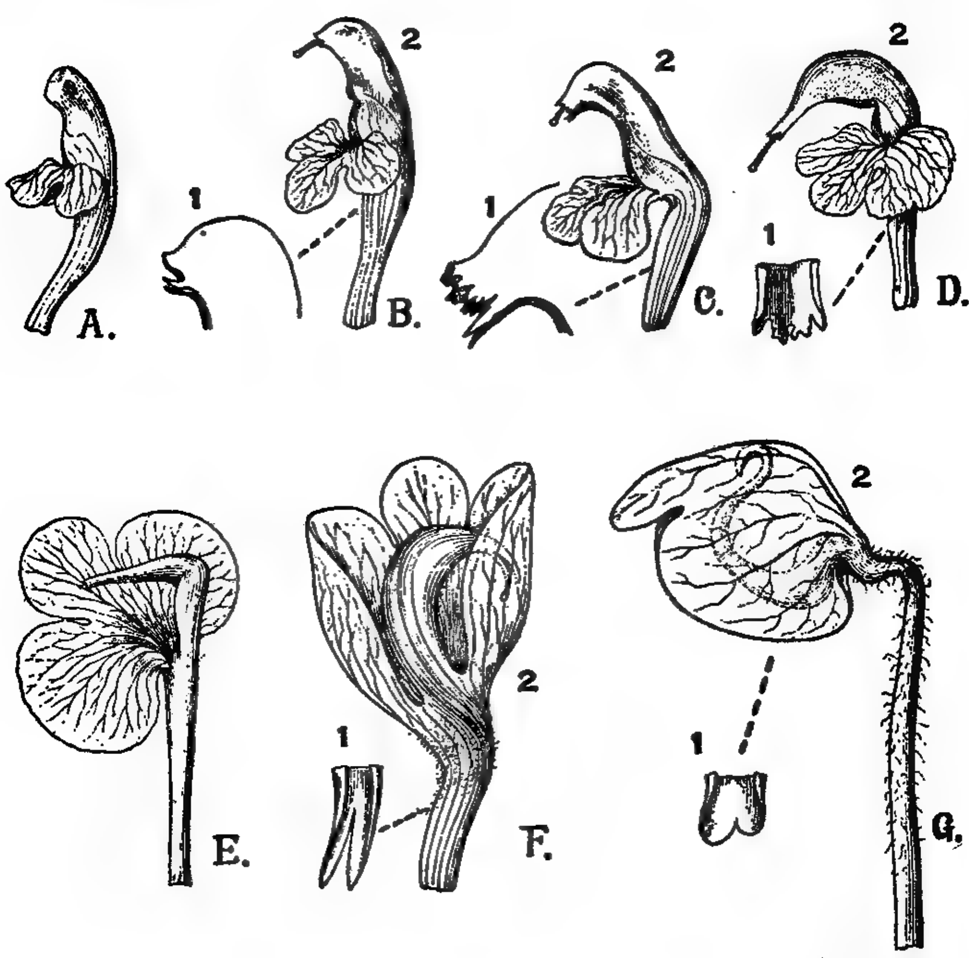


圖 2. A. *P. Oederi* Vahl; B. *P. habachanensis* Bonati; C. *P. rhynchodonta* Franch.; D. *P. filicula* Franch.; E. *P. Wallichii* Hk. f.; F. *P. Scullyana* Prain; G. *P. megalantha* Don. 1 —— 盔部頂端大大地放大(1 Apex of galea, very much enlarged); 2 —— 花部，放大一倍半 (flower, × 1 ½)。

Hurus., *P. Fletcheri* Tsoong, *P. Scullyana* Prain (圖 2, F) 和 *P. megalantha* Don (圖 2, G) 等种類來証明。

有如上述，这是極容易看出來这兩种"基本型式"对於生齒这一點上是多麼嚴格了。同样地關於生嘴方向，在这兩种"型式"的盔的形狀的改变和它的各部分所取的角度也是有顯著的區別的。像圖 2 中所示，在 *P. tristis* L. 中的盔部的特殊的弓曲，以及後繼步驟在 *P. dolichocymba* H.-M., *P. Dunniana* Bonati 等种類中所顯示的十分奇特的舟狀的構造，是專屬於 *Sceptrum* 而决不見於 *Rhizophyllum* 之中。与之相符合的是管部的相对的角度，盔的直立部分，含有雄蕊的部分和嘴的本身，在一种"型式"中是与在另一种中十分不同的。

另一种重要的徵候似与齒有關联的是盔部上的雞冠狀凸起。这一种次生的附屬物，它的作用至今不明，正像齒的本身一样地嚴格；事实上，它們是祗在 *Rhizophyllum* 和顯著地和它有親緣關係的羣中才能看到。其發現的常率，似乎与此親緣關係的远近成为正比例。当然在那一羣中間，不但最容易發生而且也達到它的最高發展；*Longiflorae* 系中的 *P. siphonantha* var. *birmanica* Bonati, *P. cranolopha* var. *longicornuta* Prain, *P. decorissima* Diels, *P. Garnieri* Bonati, *P. bella* var. *crestifrons* Tsoong 等等都是最顯明的例子。在稍稍較远的領域裏，还有 *P. Franchetiana* Maxim., *P. insignis* Bonati 等。在对生葉的羣中，我們可以找到 *P. meteororhyncha* Li 和 *P. cristatella* Pennell et Li 等。相反地，在真正的 *Sceptrum* 中，連一个生有这种附屬器官的例子都找不出來。即使在以具有"*Capitata* 型"花冠的 *Acaules* 系開始的 *Dolichomiscus* 羣中，在較進化的种類如 *P. batangensis* Franch.、*P. macrosiphon* Franch.、*P. muscicola* Maxim. 等等裏面，这方面的傾向都沒有絲毫顯示出來，虽然在外形上和花管的長度上，上述种類，都十分雷同於 *Longiflorae* 系中的种類的。

在許多將李氏的 *Lasioglossa* 組——僅僅是等於本生氏的 *Tristes* 系加上幾个相近的系——組合起來的特徵中之一，就是那些很多的、多細胞的、生在盔部边緣上的長毛[1]。这种流苏狀毛存在於我現在称为 *Sceptrum* 的羣中，而在 *Dolichomiscus* 羣中，則也在歐洲產的 *P. acaulis* Wulf 中發現。在"*Flammea*"的一方，除了 *P. foliosa* L., *P. decorissima* Diels 等种裏的有毛的盔外，沒有任何此類徵候被看到。但是在这些种類中，毛是分佈在全部的盔上的，分明具有不同的性質，而且也与所說的流苏狀毛有很不同的作用；前者也許僅为了保護花蕾使不受天气突变之害，而後者則用以留阻花粉，使不致隨意墜落而造成浪費。

(2) 下唇——除了兩个"基本型式"对於下唇所取的不同的角度外，其大小的差別，也是引人注意的。与我們行將細談的整个花部的大小，保持着密切的联繫的，在 *Sceptrum* 羣中，下唇的大小是取後退的方向的，因为在此羣進化頂點上的 *P. excelsa* Hk. f.、*P. Vialii* Franch. 和 *P. recurva* Maxim. 都有比在此羣開始時的种類小得很多的下唇。在 *Rhizophyllum* 羣中，方向却是前進的，因为唇部变得愈來愈大，一直到最進化的 *P. megalantha* Don 和它的近种，在那裏下唇是这样地發達膨大，以致於完全包裹其盔部了。

在下唇的形狀上，兩个"基本型式"也各有其特點。在"Flammea"的一面，其下唇總是比較飽滿的，常常後方較圓而無柄。在較高的种類中，它的基部常成深心臟形，这是因为那兩个很大而为耳形的側裂片，不但伸張而超过了管部的兩側，而且終於經过了盔的背部的中線，而在它的後面互相重疊起來。在最高的程度上，我們在 *P. megalochila* Li, *P. Scullyana* Prain,

---

1) 参閱圖 1。

P. megalantha Don 等种中，看到了一种形成囊狀而有類於 *Calceolaria* 屬的下唇，一种絕对不能在它的相反的"基本型式"中找到的徵侯。倒过來說，像 *P. angustiloba* Tsoong、*P. kongboensis* Tsoong (圖 3, B) 等种中的長楔形的基部和狹而尖的裂片是决不能在 *Rhizophyllum* 羣中看到的。这最特殊的例子，还是在 *P. lasiophrys* Franch. (圖 3, A)，尤其是 *P. tsekouensis* Bonati 中(圖 3, C)，在後一种裏的下唇具有長柄而以最奇異的狀态在頂部着生三个裂片。

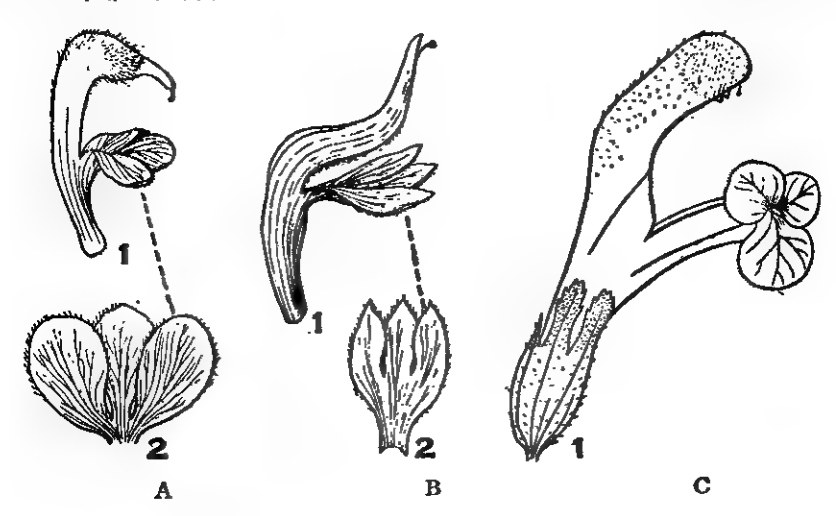


圖 3. A. *P. lasiophrys* Maxim.; 1——花 (flower), ×1½; 2——下唇 (lower lip)×2; B. *P. Kongboensis* Tsoong: 1 花 (flower), 2. 下唇 (lower lip) $\times\frac{1}{2}$(原圖, original); C. *P. tsekouensis* Bonati (李氏圖, after Li)。

(3) 管部——如像在兩种"基本型式"中所規定的，在"*Capitata* 型"中的管部是直的，而在"*Flammea* 型"中，則在近端处向前弯曲。对於这一點，要得較为清晰的印象，是还需要一些解釋的。在後一种中的管部的弯曲，似乎与花時俱增，所以常常看到掛在正成長着的蒴果上已經乾縮了的花冠管部，这样强烈地向下弯曲，以至於盔部不復向上而簡直指向下方了(相連地，長留的花冠也是那一類型的花的特徵)。在前一种型中，管部一般多是直的。但如果發現了弓曲的傾向，那麼这弓曲一定是在基部或者近基处而且一定是在萼筒裏面的。这一點是很清楚地在 *P. trichoglossa* Hk. f. (見圖 1, C)，*P. recurva* Maxim., *P. proboscidea* Stev. 等种中表示出來。这也是在兩种"基本型式"中許多强烈的对照點之一，也是唯一地曾經引起李氏的部分注意之點，他曾因而把他的 *Orthosiphonia* 組从 *Sigmantha* 組分別開來，虽然他完全錯过了这兩种型式的最初的分岐點。

由於兩种"基本型式"的下唇的不同机械作用，因而管部在進化中也顯示出某种不同的動作來。在"*Flammea*"一方，管部僅須伸直而後引長，所以管部的直徑在全長中是相同或幾乎相同的。在"*Capitata*"一方，由於下唇的直立位置，所以管部一定要經过一个初步的向喉部逐漸擴大的步驟，來使唇部達到一个地平的平面上，而管部也因之而成为多少漏斗狀了。这在像 *P. acaulis* Wulf. 和 *P. tsekouensis* Bonati (圖 3, C)，等代表本型中下唇開始伸張的种類中，是很清楚的。

至於管的長度，这斷然地只有"*Flammea* 型"(*Rhizophyllum*) 才進化到这种特殊的形

态水平的；在它相对的型中 (*Sceptrum*)，不單是那个進步得緩慢的新世界的亞羣 *Brevilabium* 現在才達到"有喙型"的初起階段 (*P. siifolia* Rydb. 和 *P. Canbyi* Gray)，即在舊世界的 *Eusceptrum* 亞羣中，也不过到達一个高度的嘴部伸長而未能將其管部作相当的引伸。这也許可以决定地說，眞正的 *Sceptrum* 羣的缺乏对於管部伸長的內在机能，比其他任何原因更能解釋它的缺乏長管的事实，而且它究竟在未來的時代裏，是否能得到这一特點，也是大成疑問的；因为这一點也許牽涉到它的花部發展，在大小上的後退和管部的扭捲等事实，因为这种步驟，可能是不利於獲得伸長的管部的。

(4) 花冠的一般大小——花的大小，在兩个"基本型式"的种類中，也是存在着强烈的对照的。在發生較早的"*Capitata* 型"种類中是較大的，然在"*Flammea* 型的同样种類中，却是確確相反。举例說，我們在前一型中有 *P. Sceptrum-carolinum* L.、*P. grandiflorum* Fisch.、*P. tristis* L. 和 *P. striata* Pall.；在後一型中，我們有 *P. flammea* L.、*P. Oederi* Vahl、*P. hirsuta* L. 和 *P. lanata* Cham. et Schl.

在進化時，这兩型也是有顯明的分歧的[1]。在前一型中一般是後退的，因为种類愈進步則花就愈小，如像在下列次序中所見的：*P. tristis* L.、*P. dolichocymba* H.-M.、*P. trichoglossa* Hk. f.、*P. lasiophrys* Maxim. 和 *P. Vialii* Franch. 在後一型中則是前進的，也可由 *P. Oederi* Vahl、*P. rhynchodonta* Franch.、*P. filicula* Maxim.、*P. robusta* Hk. f.、*P. Klotzschii* Hurus. (*P. macrantha* Klotz.) 和 *P. megalantha* Don 的次序中看出來。

2. 与"基本型式"相印証的其他形态特徵。

在对於兩个"基本型式"有了足够的認識之後，我們在这种观點下來細察其他各种特徵的時候，就開始重視原來对於分類学者沒有多少意义的徵候了。現在以它們的重要性为次序，加以詳述。

(1) 花序——馬先蒿的花序，大多是無限的，也就是向心的，但是在一个特殊的羣中，就是 *Rhizophyllum* 这个代表"Flammea 型"的羣，它却是有限的，也就是离心的。这些花在頂部或近頂处以螺旋的次序自上向下開放，在較为模式的种類中無例外地，上半部花已盛開而下半部猶在蕾中或在花期的較晚的階段裏，上部已为果而下部仍为花。这在很低微的 *P. flammea* L. 和 *P. Oederi* Vahl. 中当然很顯明，而在那崇高的 *P. elephantoides* Benth. (圖版七，上) 和 *P. bicornuta* Klotz. (圖版七，下) 中則更为清楚。在比較不很模式像 *Pumilliones* 系中的种類一般植株是幾乎处於無莖的情况之下的。如果加以細察則会發現这样一个事实，这就是在蓮座中心的蒴果，是常常先熟，所以生長較大，成熟較好而那些生在外輪的則無例外地是成熟得不够的，这是有限花序的一个可靠的表記。

相反地，对於代表"*Capitata* 型"的 *Sceptrum* 羣的開花順序則是决不会有絲毫可怀疑的。

在花葉和苞片的形狀上說來，兩种"基本型式"是存在着某种不同點的。那些十分專化了的濶卵形、常常亞全緣、密覆瓦狀的苞片是經常見於 *Sceptrum* 羣的，而 *Rhizophyllum* 羣中的苞片，一般却是葉狀而不顯著的。

(2) 体态和莖——在北極圈——那个最合理的、假設的本屬出生地——內，我們約有九种具有"無齒型"花冠的种類；这些是 *P. flammea* L.、*P. Oederi* Vahl、*P. hirsuta* L.、*P. lanata*

1) 參閱圖 1,2。

Cham. et Schl.、*P. Langsdorffii* Fisch., *P. capitata* Adams, *P. Sceptrum-carolinum* L.、*P. verticillata* L. 和 *P. amoena* Adams。在这九种裏面，最後的兩种，具有基部强烈弯曲的花管。是不能算为原始的种類的，这緣故我們以後还要加以討論。这样一來，我們就只留下來七种了，这些可以把它們分为兩組，一組包括 *P. capitata* Adams 和 *P. Sceptrum-carolinum* L. 而另一組則包括其餘五种。

在第一組中，我們見到 *P. capitata* Adams (圖版八，上) 具有短的但是却很顯明的莖，差不多裸露或者有些疏生的葉。在 *P. Sceptrum-carolinum* L. 中，莖部不但是很發達而且是時常在上部分枝的。

在第二組这些种類中間的一个共同的、很引人注意的特徵，是那优势的、時常佔有莖的大部的花序，有時甚至一直下達到那植株的基部來。在進化过程中，*Rhizophyllum* 羣自開始到中等程度 (有喙型，*Rhyncholophae*) 像 *Flammeae* (*P. Oederi* Vahl, 圖版八，下)、*Pseudo-Oederianae* (*P. pseudoversicolor* H.-M., 圖版九，上；*P. habachanensis* Bonati, 圖版九，下)、*Rhynchodontae* (*P. rhynchodonta* Franch., 圖版十，上)、*Filiculae* (*P. filicula* Franch., 圖版十，下)、*Macrorhynchae* (*P. macrorhyncha* Li, 圖版十一，上) 等系，这种体态的規律，是被嚴格地遵守着的。在較高的水平上(管花型，*Siphonanthae*) 像*Longiflorae*、*Macranthae* 等系中，則是比較不很嚴格；而在这一點上最顯著的要算 *P. elephantoides* Benth. 和 *P. bicornuta* Klotz. (参閱圖版七，上、下)，这在關於花序的論述中，也已曾涉及。

關於莖的分枝的問題 (当然这是僅指莖在上部分枝而言)，这在形态的观點上說來是有極大意义的。在研究的進程中，愈來愈觉得这个徵候，在多數情况下是与莖的木質化保有密切的联繫的，而这兩个特徵又轉而与植株的生命期的長短緊密關連。这是很容易看出的，凡那些保有其中一个徵候或兩个兼有的种類，那即使不是僅結一次果的，也至少是具有这种趨势的了。將这种看法应用到那兩个代表羣裏去的時候，在这种特徵的獲得上的先後異致，是値得深思的。在 *Rhizophyllum* 羣中，自 *Flammeae* 系到 *Macrorhynchae* 系，莖部是嚴格地保持着草質的，連下部都从不見分枝，当然談不到上部了。一直到此羣達到最高發展時，一年生的种類具有似乎木質化的莖才被發現於 *Pumilliones* 和 *Megalanthae* 系中。

在相反的一面，一种强烈的分枝情形，幾乎在 *Sceptrum* 羣剛一開始的時候就被看到，这裏 *Gloriosae* (*P. gloriosa* Bisset et Moore, 圖版十一，下) 和 *Rudes* (*P. princeps* Franch., 圖版十二，上) 系中的种類，是很好的例子。

(3) 葉——照乾燥标本上看來，兩个代表羣在葉於芽中的褶疊上也有着確定的分别的。在 *Sceptrum* 羣中，这是反捲的，而葉的裂片是和葉片本身在一个平面上的。在 *Rhizophyllum* 羣中，至少在較低程度的种類中，它的褶疊是拳捲的，一种徵候使人想起羊齒植物正在舒放的葉狀体。也許因为这种特殊的褶疊關係，所以裂片生長的角度，对葉片本身的關係，可以說是垂直的，而在舒放以前甚至在舒放後若干時間內，是以魚鰓的形式，一片挨着一片地疊置着的。但这种可作为特徵的排列方法，当这一羣的种類漸漸進化得高了的時候，就愈來愈不明顯了，而且这也只在乾燥的材料中注意到，所以在將來的野外工作中，还須要加以細緻的考証。

3. 葉序与"基本花冠型式"在作为系統的主要特徵上的对比。

在把他的思想放到系統中去時，李氏的修訂文中的三个"羣"[1] 中的第一个 "*Cyclophyll-*

---

1) 讀者請注意"羣"这个字，在李氏和我的意思中是代表着不同的階層的：在他的意思中，是代表亞屬的而在我則僅作为組。

um",包括着純粹对生（輪生)葉的种類,这些种類不但被視为一个独立的羣,而且也是被当作三羣中最原始的一羣的。他的論點的理由,引述如後:"在玄参科中,輪生的葉序,一般地多發生於在別的証候上看起來比較原始的羣中(最先出來的葉子——子葉,在双子葉中也常是对生的)。所以,对生葉的种類应当被認为較互生葉的为原始。輪生葉的情形是無例外地只在顯係古老的屬中看到……"。

李氏認輪生葉序为原始的論斷,顯然受一般概念的影响甚於事实的考校。第一,在括弧中所說的理由是幾乎沒有意义的。在植物界的進化中存在着太多的復古和重現的現象,使得有着这样遙远性質的証据成为很不現实了。很多科像忍冬、唇形、爵牀等,在双子葉中佔着很高的地位的科,是完全具有对生葉的。当然在菊科中,我們也可以看到相反的例子,在那裏对生的和亞对生的葉子,似乎比較原始,像在鱧腸、澤蘭和向日葵等屬中所見的,但是这全不能給这种理論以有力的支持;事实上,这个問題应在各个情形中加以分別的考慮。

第二,在玄参科中对生葉多發生於較原始的羣中的这一陈述,似乎正与事实相背馳。为了对於这一重要观點的闡明,我們必須將注意力移到本科中來,以求得更为直接的証据。

第一關連的当然是本科發源的問題。有兩个科是与本科有密切關係的,一是旋花科,本科中的 *Kichxia* 屬 (*Linaria* 柳穿魚屬一部)的有些种類,是和它極相像的;还有茄科,与 *Verbascum*、*Sopurbia* 等屬發生關係。这兩科巧合地都幾乎完全是具有互生葉序的。这使得玄参科从对生的葉序開始,幾乎成为不可能。

讓我們來看一下在本科中葉序是怎样的。在植物誌屬一書中,本生与虎克兩氏所給的特徵描寫是:"葉在少數屬中完全互生,在多數屬中下部的或全部对生或輪生,頂部的和花葉常常互生"。

上面的描寫是很好的,因为它全部描摹了本科中所有的三种葉序,互生的、对生(輪生)的、和那最緊要的由上面那兩种奇異地混合起來的一种,就是下部对生而上部互生,这是在本科程度較高的類型中最普遍的一种安排。

差不多用不着怀疑,本科是由互生葉的像 *Leucophyllum*、*Aptosimum*、*Verbascum* 等在花冠上並沒有專化的屬開始的。对生的葉序,初在*Calceolaria* 屬中看到,标誌着一种花部相称的变換,因为它伴隨着一个左右相称的花冠,具有很進化的下唇。从此以後,在科的較高領域內,对生的葉序就愈变愈顯著,而互生的不过在这裏那裏地散見於少數地方,它的位置是被上面所說过的、奇異的混合葉序所取而代之了。这些都無疑地表示了在玄参科中对生的葉序是由互生的進步而來,而决不是倒过來的,而在本科中这种彰著的奇特排列,則不是表示互生葉序的進化的性狀,也許就是在較少的可能程度上,表示一种对生葉的退化情形。

現在我們可以把注意力轉到馬先蒿屬本身來了。一种引起人印象的在科和屬之間的葉序上的符合點,是这三种排列,互生、对生、和奇特的互生对生混合式的同時並存。因为在 *Euphrasiae* 族的对生葉序的优势範圍內,眞正的互生葉的种類,其实只佔全屬的一小部分。在普遍地認为互生葉的种類中,一种內在的轉变为对生的强烈趨势,是十分顯明的。無數的例子可以被寫出來作为証明。例如在北美的 *P. lanceolata* Michx. 中,眞正的互生葉,非但不復成为慣例,而倒成了稀有的情形了,因为所見的标本至少是对生葉的,而連花都是对生的情形,也不算稀罕(这裏要說明,*P. lanceolata* 是被第一个專著的作者,算成对生葉的种類的)。同样地在 *P. palustris* L. (var. *Wlassowiana* Bunge, 圖版十二,下) 和 *P. sylvatica* L. 的材料中,假輪生的枝葉,是並不特出的。如同在*P. resupinata* L. 和它的近种*P. yezoensis* Maxim. 情形一样,对生葉子是十分普遍的,前一种的亞种 subsp. *oppositifolia*(Miq.) Tsoong 是一个很好

的代表。再者，拿对生葉的 *P. rigida* Franch. (圖版十三，上)和其近种*P. comptoniaefolia* Franch. (圖版十三，下) 兩者都具有很堅挺而分枝的体态，乾時变黑的顏色，披針形淺裂或近全緣而齒多胼胝的葉子，有顯著苞片而緊密的花序，有少數鈍齒而單面開裂的萼和相当伸直的花管，來和互生葉的种類如 *P. corymbosa* Prain (圖版十四，上)、*P. nigra* Vaniot (圖版十四，下)等相比較，就会發現在大部特徵中，除了葉序以外，前者与後者是極相近似的。这是很足够來說服任何人，它們之間的相似，是由於眞正的親緣關係，而决非是發展中偶然發生的並行現象所形成的。与此情形相類似的是以 *P. salicifolia* Bonati 对 *P. nigra* Vaniot, *P. Mairei* Bonati (圖版十五，上)对 *P. palustris* L. (參閱圖版十二，下)，*P. verticillata* L. (subsp. *latisecta* Tsoong, 圖版十五，下)对 *P. sylvatica* L.、*P. labradorica* Wirsing, *P. canadensis* L. (圖版十六，上)等等。*P. verticillata* L. 的萼和蒴果，也是極端地接近後面三种的。它們相互之間的關係，是与 *P. resupinata* L. 和它的对生葉類型之間所存在着的相彷彿。

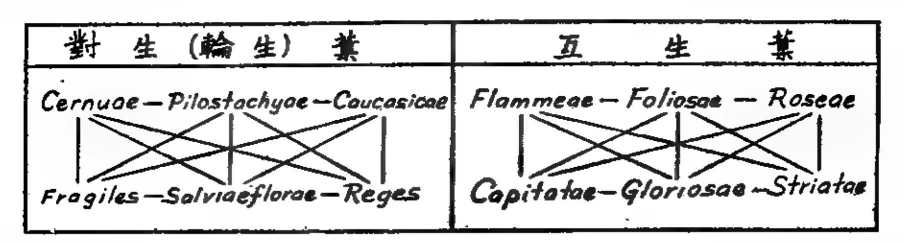
这些例子不但有力地証明了对於不同葉序的羣各自進化的推測之不可靠性，同時还確定地表示了对生葉的羣是从互生羣中進步而來。

在从前，見到了輪生葉的种類比对生葉者佔絕大多數，所以後者僅僅被認为附屬於前者，而沒有注意到後者在大多數的例中，反係前者的先驅者。而这也是有充份的証据足以証实它的。差不多在 "*Cyclophyllum*" (輪葉亞屬)中，有半數以上的羣是以对生葉開始的，因为在各該羣中，具有对生葉的种類無例外地都是比較原始的。所以在各个羣和亞羣中的開始的一系，如 *Cyclocladus* 羣中的 *Salviaeflorae, Fragiles* 和 *Aloenses* 系，*Eubrachyphyllum* 亞羣中的 *Lyratae* 系，*Rigiocaulus* 亞羣中的 *Salicifoliae* 系，*Eudolichophyllum* 亞羣中的 *Cernuae* 系等，不是全部也至少是一部对生的。也可以看到在兩个"基本花冠型式"的各自的一面，那些以对生葉的系開始的各羣，在親緣上說來，是要比以輪生葉的系開始的各羣，要更緊密地靠近它們的互生葉的祖先。所以，以具有离心花序的 *Cernuae* 系 (*P. cernua* Bonati, 圖版十六，下)開始的*Dolichophyllum*羣，是要比以具有向心花序的 *Caucasicae* 系開始的 *Orthosiphonia* 羣更近於 *Rhizophyllum* 羣。同样地，在 *Cyclocladus* 羣開端处的 *Salviaeflorae* 系 (*P. salviaeflora* Franch., 圖版十七，上)要因为具有較大的、無齒的花冠，和疏散的、对生的枝而比 *Cyathophora* 羣中的 *Reges* 系，更貼近於 *Gloriosae* (參閱圖版十一，下)。而且在葉序的自对生变为輪生上，也还有蛛絲馬跡可尋。很可以說 *P. salviaeflora* Franch. (圖版十七，上)与 *P. floribunda* Franch. (圖版十七，下) 兩种間的親緣關係是不容置疑的，但是前者是对生葉的而後者則已進步而得到了確定的輪生葉序了。在有些种類中，对葉和三枚輪生葉同時並存的情形是很昭彰的，如在 *P. verbenaefolia* Franch. 中一般。但在它的近种 *P. Smithiana* Bonati 中，葉已完全是輪生的了。在靠近 "*Flammea* 型" 的系如 *Caucasicae* 系和 *Cernuae* 系中，可以在 *P. sarawschanica* Maxim.[1] 和 *P. cernua* Bonati 兩种裏看到一种奇異的現象。在这裏，对葉和輪葉的情形，同時並存於同一植株之中，这就是葉对生而花輪生。照我所能理解的，除了在 "*Flammea* 型" 中的离心的花序，使得葉序的变化取一个顚倒的程序，所以苞与花先於葉变为輪生之外，似乎再难找到更適当的解答了。

对於分析葉序这一點上已經說得不少了，現在讓我們來看一下以葉序为基礎的系統，与以"基本花冠型式"为基礎的系統之間，实际上存在着的區別吧。在假定輪生葉和互生葉各羣，都係

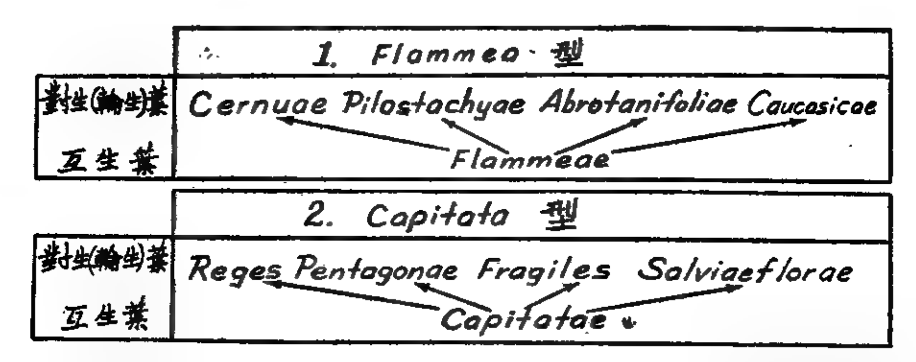
1) *P. sarawschanica* Maxim. 原被其命名者作为互生葉的种類，但在看了原种标本後，就很消楚地看出它是对生葉的。

各自独立地進化的時候，看起來李氏似乎認为同在对生（輪生）葉序內的，屬於“*Flammea* 型”的 *Cernuae*、*Pilostachyae*、*Abrotanifoliae*、*Caucasicae* 等系，和屬於“*Capitata* 型”的 *Salviaeflorae*、*Fragiles*、*Pentagonae*、*Reges* 等系之間的親緣關係，要比在前面的四系和互生葉中“*Flammea* 型”的 *Flammeae*、*Roseae*、*Comosae* 各系之間的，或者是後面的四系与互生葉中“*Capitata* 型”的 *Gloriosae*、*Capitatae*、*Striatae* 各系之間的關係，更为密切似地。这样的安排方法，祗造成將保有密切關係的單位，互相脫离，同時却反將關係很疏的單位，武断地放在一起。請參看下面的表格：



如果提出一个問題，無論在对生(輪生)葉或者是互生葉的範疇內，到底还是“*Flammea*”型的各系，演化为“*Capitata* 型”的各系來的呢，还是倒轉來的呢？要得出一个合理的解答，就無疑地將成为一个大难題了。与此相联的是給与在互生葉中的对生葉亞种，像 *P. resupinata* L. subsp. *oppositifolia* (Miq.) Tsoong 之類，以一个適当的安插所引起的困难，而这个亞种在李氏的修訂文中，是顯著地付諸缺如的。

与以上相对照的，讓我們再來看一下第二表格：



上面的表格在这兩个“基本型式”中的各自的互葉和对葉系之間的內在联系，給人以一个清晰的印象。这裏再來着重指出它們是怎样地在改換葉序時忠实地固守着它們的花冠型式，似乎有些多餘了。此外营养器官中的某些特徵，是如何地与花部構造相契合，也是很看得出來的。在一面，那些 *Gloriosae*（參閱圖版十一，下）系中的种類的高昇而有疏枝的莖，默証了它們与 *Salviaeflorae*（參閱圖版十七，上）和 *Fragiles* 系間的極近的親緣；在另一方面，那 *Flammeae* (*P. Alberti* Regel, 圖版十八，上；請再參閱圖版九，十）系中的特殊的具有佔优势的花序之短莖，也明白地指向着它的在*Caucasicae* (*P. pycnantha* Boiss. subsp. *tenuisecta* (Lipsky,) Tsoong 圖版十八，下）与 *Cernuae* 系中相对的种類。

存在於本系統与以前的以“進化花冠型式”或葉序为基礎的系統之間的主要的不同，是在於

我們是以現在所能得到的材料为依据的，一种每个植物学家都应達成的目的。替代了空想的、不現实的麗納蒂氏的“古代馬先蒿”，“古代無齒型”等等作为出發點，我們是可以相当準確地指出：即使 *P. flammea* L. 和 *P. capitata* Adams 不是它們各自羣中的眞正最老的祖先或是祖先的原型，至少它們也是現存种類中的最老類型。

除此之外，把对生葉的种類放在互生葉羣中的事实也变得更合於邏輯，因为它們是被視为尙未確立对生葉特徵的類型，而它們的眞正对生葉的親屬，是可以在貼近的羣中找到的，而不至於被安排於認为毫無關係的遙远的羣中去。

（二） 本屬在進化中的其他重要點

在前面的論述中，我們主要是注意於那兩种“基本花冠型式”的區別，和除了花部構造之外的器官所顯示出來的印証。这裏我們將要來看一看全屬裏面的進化趨勢，在这裏面也有与上面所闡明的“基本花冠型式”相衝突的地方；也有些是在我們研究中所看到的某些在發展中的特殊情形。这些是可以下列的分類來說明的：

1. 特殊的進化方式

在本屬內，常發生特殊的進化方式。这裏面有的是与某些較高分羣的建立和安排有着極緊密的關連的，所以需要再加說明。其中主要的兩點如下：

(1) 莖——以前我們已經粗略地討論过表示在木質化和分枝方面的莖的正常進化过程。在这裏，我們將注意到進化的負的方面的情形。大多數以前的作者，都以为 *Acaules* 系，按照它名字的意义，是表示一种原始型的、由此發生本屬中所有具莖种類的祖先。对於这样的假定可以有兩點非难。第一，在花部的構造上，就是在已經相当伸展的下唇和与此相連的花管喉部的膨大上，它是分明地要比 *Capitatae* 和 *Gloriosae* 兩系中的种類較为進步。第二，像上面所引的後面一系一样，由它的地理分佈上，可以看出毫無疑問地屬於“間冰期—溫暖植物型”的。依以前所談，在北極圈內的眞正的原始种類中，我們祇看到兩种類型的莖，我們就很有理由來把这种無莖的、以異常伸長了的花梗，來代替被抑制了的主莖的作用的这种情况，不作为原始的徵候，而当作是進步的表現。因为不但同样的現象在許多例子中重複，最明顯的如像在 *P. decorissima* Diels（參閱圖版二十二，下）中，而且更以由此進化成为一个特殊的羣——*Dolichomiscus* 羣的事实，來証实这一點。在生於亞洲而与歐洲的 *P. acaulis* Wulf（圖版十九，上）相对的 *P. Artselaeri* Maxim. 之後，*Vagantes*系的單种的 *P. vagans* Franch.（圖版十九，下）已經開始了一个將在下一系 *Longipedes* (*P. filicifolia* Hemsl，圖版二十，上）中变为主要徵候的步驟，那就是生出具有腋生花的長而匍匐的新条來，虽然它仍保持着前面一系內遺留下來的具有長柄的基出花的特徵。不过这种中間階段，隨即为在 *Longipedes*, *Batangenses* (*P. batangensis* *Bur. et Fr.*，圖版二十，下）和 *Muscicolae* 等系中所見的基生花完全消失而花全生在長条葉腋中的一种情形所替代了。

(2) 花冠——在以前，*Verticillatae* 系的种是時常被認为係对葉种類中的最原始的一類，於是就武断地被作为所謂“輪葉羣”(*Cyclophyllum*) 的祖先，这对於这一系來說，眞可以說是最不相称的負担了。

李氏在部分地看到了管部的分別之後，就把管子在萼內弯曲的 *Sigmantha* 組和管在萼內伸直的 *Orthosiphonia* 組分別開來。但是由於僅僅滿足於現象本身的观察，所以就未能追尋 *Sigmantha* 組內这一管部特殊構造的起源。

像在前边說过的，如果"*Capitata* 型"裏的管部有弓曲的傾向時，这現象常常發生在基部附近而在萼内的；*P. trichoglossa* Hk. f. 等种類可以为証。在这以後，我們看到在互葉的种類中像 *P. labradorica* Wirsing、*P. lapponica* L.，和对葉的种類中像 *P. floribunda* 与 *P. rigida* Franch. 等等，都表現出在管部中有同样的徵候。

李氏曾合理地解說花管的弯曲，是植物本身傾向於使昆虫易於落下的表示，而他的意見，似乎是完全切合植物在这一特殊器官中所採取的各种進化步驟的。如果我們將 *P. corymbosa* Prain, *P. comptoniaefolia* Franch. 和 *P. spicata* Pall. 三种並放在一起，我們就会立刻注意到这三种在一般形态方面的相類，和在另一方面的三种管部弯曲的不同的程度。这一點很充份地証明了我的不以 *Verticillatae* 系为一个程度較低的羣，而当它是一个單独地採取了一种特殊進化路線的羣的意見[1]。

盔部一般進化的趨向，在与下唇相对照的長度上，可以說是退步的，这就是說一个种類愈進化，它的盔部就愈短；这当然是只指盔部的直立部分而言，因为在較進化的种類中，上面一段，是常常横伸为嘴部的。所以所有較原始的、在各羣中開端的种類，都具有高超於下唇的盔部。而在 *Sigmantha* 羣中，一般的下唇的擴大和伸張，特殊的管部的弓曲是一定与这一點保持着密切的联繫的。如果管部的弓曲可以解釋为一种進步的表記，那麼，盔部的短縮也必須是指向同一趨势的，因为当然一个較短的盔部是会比高蓋在下唇上的盔部更容易使昆虫來降落的，这至少在 *Verticillatae* 系裏是如此的。照此推論，則凡本系内的具有短盔的种類如 *P. likiangensis* Franch., *P. holocalyx* H.-M., *P. spicata* Pall. 等等，是 *Sigmantha* 羣裏的頂極類型而不是如一般地以为这是一种最原始的模式[2]。

除了以上所述之外，还有其他的許多現象曾經注意到，可以論說如下：

2. 進化中的並行現象

在研究本屬時，時常遇到的特別有趣之點，就是屬於不同羣的种類中，發現並行發展的現象。在这裏边最完全的例子，也許是屬於下述的兩种，这就是 *P. striata* Pall.（圖版二十一，上）和 *P. elata* Willd.（圖版二十一，下）。在表面上看來，它們之間的一般体态、高度、葉形甚至於花序的長短的相似，使我們有充份的理由，認它們为極其親近的种類，这也是为什麼它們在李博士的修訂文中，被同放在 *Apocladus* 組中的緣故。但是在一檢查了花冠之後，就会立即發現这兩种在親緣上是不相靠近的，因为它們是屬於兩个相对立的"基本花冠型式"的。前者具有"*Capitata* 型"的花冠，是 *Nothosceptrum* 羣中的一种而後者具有"*Flammea* 型"的花冠，才眞实地屬於 *Apocladus* 羣。在發展時，前者進化为 *Proboscideae* 和 *Recurvae* 系，而後者和它的近种 *P. sudeticae* L. 和 *P. scopulorum* Gray 進化成 *Compactae, Incurvae* 和 *Surrectae* 各系。

那个單模式的，以具有長梗基生的花和在長而弱的新条上腋生的花而將 *Acaules* 系連接到 *Longipedes* 系去的 *Vagantes* 系（參閱圖版十九，下），也並非是一个孤立的例子，因为它的具有或多或少同样徵候的極相似的相对种，可以在 *Corydaloides* 系（*P. corydaloides* H.-M.，圖版二十二，上）中找到。虽然它們兩者之間的外形是这样地相似，以至为李博士放在相近的羣中，但是在这兩个系的花開程序上看來，把它放在一起是絕对不合理的，因为在前者的新条上的花，是向心而開的，而後者的却是肯定地离心的。这無疑地是表示在兩个完全不同的羣内的並行發展，因为一个是近於"*Capitata* 型"的，可在 *Dolichomiscus* 羣的始自 *Acaules* 系中看出，

---

1) 參閱李氏在 *Verticillatae* 系下的討論（修訂第一部 300 頁）。

2) 參閱在後面的分類系統中 *Microphyllae, Verticillatae, Melampyriflorae* 等系内的种的排列次序。

而另一个則是与 *Flammeae* 系本身十分相近的，可在開花程序和花的形式上看得出來。

与上述相類似的还有 *Acaules* 系与 *Longiflorae* 系中的某些种類如 *P. decorissima* Diels (圖版二十二，下)等等之間的情形。它們之間的表面上的類似，决不应視为眞正親緣的接近，而应該看成是因並行的發展才如此的。

以上的例子，是在相互間缺少關係的各羣中所見的並行現象，它們大部僅僅表示了一些不連貫的事实，而这些只能認为係偶然發生的巧合，而並無一定的血統意义的。另外一种更有兴趣的例子，是在兩个有着很近親緣的羣 *Sceptrum* 和 *Cladomania* 之間發現。这裏的並行現象是这样特出地表現出來，以至於在一羣中的某些特徵，再一次地在另一羣中一點不差地重新出現一遍。这种例子就不应僅僅地被看做一种普通的並行現象，而应拿來表示在相近羣中的進化趨势的相伴，这就是說，从同類的祖先發生，並且已經確切地分化了來走各別的進化路線之後，兩个羣仍舊在某些特徵中互相比拟，甚至於達到像在本例子裏所見的即使在進化的轉折點上也相符合的这样的細緻程度。

在 *Eusceptrum* 亞羣中的 *Gloriosae* 系，包含一个廣佈歐亞的 *P. Sceptrum-carolinum* L. 和在日本的其他种類，是具有乾燥時綠的顏色，和基部很寬的下唇。在其相近的始自西伯利亞而下來到中國，和喜馬拉雅的 *Tristes* 系(廣义的)中，一种乾時黑变的顏色，和强楔形的具有較狹裂片的下唇就标誌着一个新的開始點，这在許多种如 *P. Clarkei* Hk. f., *P. angustiloba* Tsoong 和 *P. kongboensis* Tsoong 等中所見的。如果我們再以 *Cladomania* 羣來相比較，我們会看到这兩羣的進化中存在着可驚異的並行現象。这一羣，以 *Hirsutae-centripetae* 系自北極圈內開始，在歐亞以 *P. palustris* 和 *P. resupinata* L.，而在北美則以 *P. lanceolata* Michx. 为廣佈的代表。那裏在乾燥顏色方面很少变動(除了北美的 *P. crenata* Bth. 有变黑趨势)而在下唇形狀也無異致，因为大部是圓形的。但在到達中國南部的時候，上述的兩种徵候，就開始在 *Carnosae* 系的种類中出現，而这一系也同样地是这一羣中轉折點的里程碑。本系中第一种 *P. nigra* Vaniot (以前放在 *Racemosae* 系中，現在移至 *Carnosae* 系) 的种名就足以表示它的黑变的趨势，如果同時再檢視一下这一系內种類的下唇構造，就不可能不看到在第二點中的共通处了。

3. 在進化中的特徵返祖現象

在植物界正常的或正的進化規律中，看到後退的或負的步驟，是很尋常的事，而在本屬中也非例外。这样的步驟，一般常表現在某些早已在过去的時間內，經过進化的分歧作用而久已消失了的特徵的重現。

虽然粗淺地看來，具有相同的現象和表面的價值，在本屬中看到的返祖現象，却似乎可以分为完全不同性質的兩類。在有一些植物裏，單个的或數个特徵的重現，是僅僅屬於一种孤立的不相連續的性質，而不再進而影响進化的趨向；这样的消失了的特徵的重現，祇能被認为一种停止了的或者靜止的動作。所有这种情形，都屬於第一類。在另一些植物裏，不像第一類，重現的特徵是不屬於靜止的性質的，而相反地表示着一种進化的動力，因为在这种的返祖現象之後，常常有在这一羣裏發現明顯的返老还童而進化又形活躍的情形的可能。

对於第一類，这裏可以举幾个例子。

我們在前面已經詳尽地討論了从对生而变为輪生的葉序的進化。这样从对生的 *Salviaeflorae*系(參閱圖版十七，上)，*Eucyclocladus* 亞羣就按進化的程序，進入到輪生的 *Melampyriflorae* (*P. floribunda* Franch.，參閱圖版十七，下)、*Longicaules* (*P. Dielsiana* Bonati,

圖版二十三，上)、*Graciles* (*P. gracilis* Wall. subsp. *stricta* Tsoong, 圖版二十三，下)和 *Coniferae* (*P. conifera* Maxim., 圖版二十四，上)等系。但是在親緣線的那一头，却發現了一个具有对生的枝、葉和花的類型，这就是 *P. gracilis* Wall. subsp. *genuina* Tsoong[1] (圖版二十四，下) 它的長而細、多少弯曲而对生的枝，以及它的葉形給它以一种印象，能使人立即就想起 *P. salviaeflora* Franch. 來。

在花部發展上，也有一个不尋常的，局部退回成原始型的例子，而这是在苏里埃無号 (1892) 的一張标本中發現的。我們知道这張标本所屬的*P. rhynchodonta* Franch. (圖 2, C)，它的盔部已經達到了一个具有短嘴，並生着一对主要的和幾个較小的附屬齒的中級進化類型了。在这一特殊的标本中，位於离心花序頂部下面的一个花，突然地回復了和 *P. Oederi* Vahl 相同的“無齒型” (*Anodontae*)。

上面的例子，不但在性質上，因为看到 *Graciles* 系与 *Salviaeflorae* 系相距之远，和“無齒型” (*Anodontae*) 是被“双齒型” (*Bidentatae*)[2] 从“喙齒型” (*Rhynchodontae*) 隔開來的事实而感到特殊，而且也因顯示了原始的和較進步种類之間的錯綜的關係而使分類学家感到特殊的兴趣。

对於第二類，我們也可举出一个最富啓發性的例子來。在 *Cladomania* 羣中的 *Palustres* 系、大部的种類如 *P. sylvatica* L., *P. palustris* L. (参閱圖版十二，下) 等都具有細裂的葉子。从以生有深羽狀分裂的下葉，和亚全緣，或細淺重鋸齒的上葉的 *P. labradorica* Wirsing (圖版二十五，上)为标誌的轉折點之後，羽狀細裂的特徵，完全变为隱伏了。一直等到这一羣進步至 *Microphyllae* 系的時候，这一特徵，才在 *P. tenuisecta* Franch. (圖版二十五，下) 中重現。在一般体态上，拿这一种來和 *P. palustris* L. 比較一下，就会發現这种的莖部的木質化，幾乎是这兩种間在营养器官中的唯一區別了。在 *P. tenuisecta* Franch. 中所見的，事实上标誌着这一羣的一个新轉折點，因为从这一种中又發生出好許多新的种類來，从而使这一羣变为更加繁荣。

4. 在進化中的一些矛盾現象，和对它們的可能解釋

以上我們祇提及了这兩个以 *Rhizophyllum* 和 *Sceptrum* 为代表的“基本花冠型式”之間的尖銳的分界。如果在整个屬中，这种界劃保持同样尖銳的話，那麼來求得一个自然的系統，將自然地成为十分簡單了。但是事实的表現却是恰恰相反。不但各羣在昇到較高的進化水平時，这种对照很快地減弱下來，而且在各羣与这兩个代表羣愈相疏远的時候，也發現有同样的情形。在这以外，甚至於有某些正与我們所規定的兩种“基本花冠型式”相衝突的情形發生。依照所表現出來的現象看來，有一些困惑的情形，似乎是可以歸之於一般的進化趨勢的輳合性的。有幾个認为是这样的例子可以列举如下：

(1) 花冠——盔部的一般發展方向，是將其頂部伸長为嘴，这种步驟是为兩种“基本型式”所共有。以下唇來講，很明顯地“*Capitata* 型”的前進，是从直立的位置漸漸開展，以終達於一个地平的位置。兩种“基本型式”中的嘴部的伸長，再加上了“*Capitata* 型”一方面的下唇的伸張，就在進化線上造成了一个中間領域，在这裏面，花冠的區別变成模糊不清了。这种辨認確切

1) 請参閱在分類系統部分中的 *P. gracilis* Wall. 下面的論述。

2) 这裏还須叙明所謂“双齒型”事实上是包含着兩个較小的進化階段的，这就是一个有角的型式，为 *P. pseudoversicolor* H.-M. 所代表，和一个眞正的双齒型，为 *P. kabachanensis* Bonati 所代表。

"型式"的困难，更因花冠大小中所存在的類似情形而增劇；这兩种"型式"的花冠大小和進化，虽然正好相反，然而到了一个特殊的水平——就是"有喙型""*Rhyncholophae*"——中，也因交叉而互相遇合了。这就是那些較早的，在低程度的範圍內相当認清了"基本型式"的作家們，到了这一點上就不再能緊緊地抓住兩者的區別，而開始將所有种類，都歸入到那个混雜的"*Rhyncholophae*"(有喙型)裏去的緣故。

(2) 花序——那各自的開花順序，*Rhizophyllum* 离心而 *Sceptrum* 向心，是絲毫沒有疑問的。但是，進化的方向也分明是單方面的，那就是 *Rhizophyllum* 是朝着向心發展的。虽然在眞正的 *Rhizophyllum* 裏面，这种特殊的离心的花序是一直被帶到最高的發展中，像 *Megalanthae* 系中的 *P. elephantoides* Benth.(圖版七，上)和 *P. bicornuta* Klotz.(圖版七，下)，但是相去極近的 *Rhizophylliastrum* 亞羣中，这种特徵，已然部分地失去了。有些种類像 *P. yunnanensis* Franch.、*P. rhinanthoides* Schrenk和 *P. Franchetiana* Maxim. 等，除了它們的常常向心的花序外，是和 *Eurhizophyllum* 亞羣中同等程度的种類極其相似的。再在稍远的 *Apocladus* 羣中，則開花順序就完全变为向心，而不易与"*Capitata* 型"中花序相區別了。

(3) 体态——一般的意見，都以为一年生的是比多年生的为進步，而这一點在本屬中看起來是完全相合的。这一徵候，似乎也是全屬的進化目标，虽然各羣在这一點上所達到的程度各有不同。在多年生佔优势的 *Rhizophyllum* 羣中，祇有最高程度的系像 *Pumilliones*、*Megalanthae* 裏面的种類，才有結單次果或者是一年生的种類。在相对的 *Sceptrum* 羣中，一年生的趨势，不但發現較早而且也顯佔优势。在中間的一些羣中，那些与 *Rhizophyllum*、相距得远些或者可以說与 *Sceptrum* 近些的羣中，是在这一徵候中比較顯著的，所以 *Cladomania* 羣在單次果的种類的百分比上是較高的，輪生葉各羣中也比互生葉各羣中要多些。这一點在較高的進化水平上，为一个种類找到比較合宜的分類位置上，也多少增加了一些困难。

这种天然輳合的發展趨勢，固然供給了本屬中所見的困惑現象以一部分的答案，然而这是不足以解釋一切的。而这对於某些与我們的"基本花冠型式"相衝突的事例所引起的疑难，尤其不足以給与滿意的解答。要了解这些矛盾現象的性質，我們必先以易於把握的形式，把各种例子介紹出來。这些主要的条例如下：

1) 盔部的齒——这是一个使較近的一些作者，最感到迷惘的一个問題。在所有的生齒的情形中，尤以那神秘的"双齒型"(*Bidentatae*)更为困惑。麗納蒂氏在形成了他的思想中的主要的兩點——"双齒型"与他羣中缺乏雜交的情形，和在 *Tristes* 系(最廣义的)中並無有齒种類——之後，他就推断以为"双齒型"为一独立之羣，所以得出他的1918年的系統來。

李氏似乎也曾感到相当困难來决定究竟那一种为屬中的最原始的花冠型式，是"無齒型"呢，还是"双齒型"呢？在我們的研究中，我們已經得到了確定的，而且部分地与麗納蒂氏相同的結論，那就是在 *Sceptrum* 中，盔部的發展，不經过有齒的階段而 *Rhizophyllum* 則为模式的生齒羣，虽然它事实上也是以無齒的類型開始的。但是李氏的猶豫不定也並非沒有一些緣故的，因为有些天然的忽隱忽現的双齒花冠，要得到滿意的答覆，实在也是極端困难的。如要举例，当以 *P. szetschuanica* Maxim.[1] 与 *P. rex.* C. B. Clarke[2] 相对比为最宜。前一种屬於 *Verticillatae* 系的，那裏面無齒的類型佔絕大的优势，而这是唯一的突然發現盔端有稜角和齒的种類。这种在無齒範疇內突然出現有齒的類型，似乎表示着这齒是遺傳下來但是隱伏着的一种徵候。相反地，在 *Reges* 系中，所有的 *P. rex* C. B. Clarke 和它的近种的正常類型都是

有齒的，而它的 var. *Rockii* Li 大約是唯一的盔上無齒的情形了。

此外，在許多例子中，我們更看到了一个模式的 "*Capitata* 型"的花冠，上面却長着兩个齒，如像在互葉羣中的 *P. hirtella* Franch.、*P. pteridifolia* Franch.、*P. striata* Pall. 等等和对葉羣中的 *P. fragilis* Hk. f.、*P. rex* C. B. Clarke、*P. melampyriflora* Franch.，*P. rigida* Franch. 等等种類。

2) 下唇——在下唇的位置上，也存在着一些模稜的情形。*Palustres* 系，作为一个單位，在花冠形式上是不一致的。*P. palustris* L. 和 *P. labradorica* Wirsing 具有相当直立的下唇，幾乎与 *P. lanceolata* Michx.——一种被史蒂芬氏放在他的 *Personatae* '族' 中的种類——完全相等。相反地，在他們的近种 *P. sylvatica* L. 和 *P. lusitanica* Link et Hoffm. 中，下唇是幾乎以直角伸張的，这个事实，不但在乾标本中看到，而且在前面一种中，也在野外親自观察过。但是，这些种類的親緣關係，却是無容置疑的！

3) 花管的長度和弯曲——由確切的事实中，我們看到了，像在盔部的齒一样，在眞正的 "*Capitata* 型" 中 (*Sceptrum* 羣的主要發展線)，並沒有一个种類，曾經得到一个相当長的，能与 "*Flammea* 型"中的 *Longiflorae* 与 *Megalanthae* 兩系相比拟的花管；在事实上，种類愈進化，則其管反愈短。但是，在以 *Acaules* 系內盖有不可能被錯認的、生有長緣毛的盔和直立下唇的烙印的歐洲种 *P. acaulis* Wulf. 为首的 *Dolichomiscus* 羣中，那些在最進化的 *Muscicolae* 系裏的种類，却很佔优势地和 *Rhizophyllum* 羣中相等的种來作管長的競賽。这是在互生的葉序中。在对生葉序中，又有 *Cyathophora* 羣中的 *P. cyathophylla* Franch. (参閱圖版二十七，下)和 *Asthenocaulus* 羣裏的 *P. flexuosa* Hk. f. var. *longituba* Tsoong，也顯示了相当長的管部，虽然它們各自的原始种類 *P. rex* C. B. Clarke (圖版二十六，上)和 *P. fragilis* Prain 除了盔上有齒这一點外，是具有典型的 "*Capitata* 型" 的花冠型式的。

上面所列的例子，很好地表示出問題的複雜性來。除非我們預备漠視事实而不問究竟，那我們就一定要瞭解这些奇異的現象是怎样來的。为了这，我們必須首先決定一个問題，就是本屬的進化，还是歧分的呢，还是輳合的呢，那就是說还是中間型羣中的一个，生出所有其他各羣，以至最終發展成为現在有着尖銳區分的兩个代表羣 *Rhizophyllum* 和 *Sceptrum* 的呢，还是正相反呢？如果作为歧分的吧，那麼，这將要成为十分困难，來指定任何一个中間羣如 *Apocladus*, *Cladomania*、*Orthosiphonia*、*Sigmantha* 等，來作为本屬的創始者，因为無論在形态的特徵上，抑或是地理分佈上，終是存在着一些可以非难之點，使得这样的指派成为不合理。相反地，所有的表徵，似乎都指向着一个輳合的進化，因为在形态上最原始的种類，都集中在这兩个代表羣的各自的開端处，更有在植物分佈观點方面的証据來加以証实[3]。

---

1) var. *angulata* 和 var. *dentigera* 是 *P. szetschuanica* Maxim. 的兩个变种，在哈雷斯密斯氏採集的中國玄参科植物一稿中寫出，这稿原拟在 Upsala 植物園刊物 Symbolae Botanicae 中發表。

2) 在 *P. rex* C. B. Clarke var. *Rockii* (Bonati) Li 下面，李博士直截地將齒解說为原來联合而为盔部的兩个花冠裂片的中脈的凸尖。照他說这不是一种後生的器官，所以它的存在是表示原始狀态的。这是由於在这个特殊的例子中，齒的生長是表現在負的方向的關係。这种看法是与他自己在 234 頁所表示的意見，大部矛盾的；而且也与他在 Rhizophyllum 組中的排列相衝突，因为在那裏面有齒型是放在無齒型後面的。至於齒的眞正來源，在仔細察看後感覚到很难決定。在我的意思，以为有時在盔的前緣出現的，形成"喉齒型"的齒或耳，也同样地，而且也許比端下的齒能更確当地被看做花冠裂片的伸出中脈。

3) 請参照地理分佈部分。

当所有現存的証据都指向一个輳合的進化時,那麼,可能有一些已然滅絕了的种類,会生出这兩个花部和其他伴隨特徵有着这样根本差異的羣來的可能性是更少了,理由是种類愈原始,它們之間的差別愈大、也愈尖銳。

如果所有的一个單元發生和分岐進化的可能性,都为事实所駁斥,那麼我們將被迫接受一个假定,以为本屬是兩元的,也許是由較低的科中的某屬的兩个不同的种發生出來的。

虽然在大部的顯花植物中,存在着种間不孕界劃,人們还是不能不在一个兩元的基礎上,提出一个假設,在發展的初期[1],在北極圈內处於比較統一的环境条件中,並且保持着密切的接觸,在兩个相对的"基本型式"的种類之間,發生了雜交,因而生出一些不很嚴正的种類來,这些,在後來往返遷移的時候,在改变了的环境之下,分化为許多中間的羣,而这兩个原有的類型,却仍然繼續發展以至今日,如像我們在 ***Rhizophyllum*** 和 ***Sceptrum*** 兩羣中所見的一般[2]。

---

1) 这裏要說到的是由地理分佈上得出的結論, *Sceptrum* 羣是要比 *Rhizophyllum* 羣出生得晚的多。

2) 由於王伏雄教授的协助,我曾檢視了三种馬先蒿的花粉。这三种裏面, *P. Sceptrum-carolinum* L. 和 *P. tristis* L. var. *macrantha* Maxim. 是屬於"*Capitata* 型"的,而 *P. Oederi* Vahl var. *heteroglossa* Prain 是屬於"*Flammea* 型"。这兩种不同的"基本型式"的花粉,不但大小差得很多,而且它們的構造也相去很远。下面是兩个种的花粉的描述:

1. *P. Oederi* Vahl var. *heteroglossa* Prain
花粉扁球形, 17.20 (16.92—18.33)×20.30 微米 (19.74—21.15) (20 个平均)。具三溝,在極面滙合,成为合溝。外壁光滑(圖 4, A)。

2. *P. tristis* L. var. *macrantha* Maxim. 花粉略扁, 29.33 (26.79—32.43)×31.56 微米 (31.02—33.84)(20 个平均)。具三溝,三溝分离,不形成合溝,溝边不明顯。外壁具顆粒(圖4, B)。

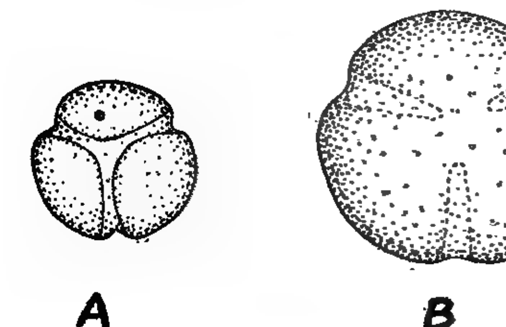


圖 4. A. *P. Oederi* Vahl var. *heteroglossa* Prain; B. *P. tristis* L. var. *macrantha* Maxim. (×1000)。

在爱特門氏的"花粉形态和植物分類"一書中 (1952), 共有七种馬先蒿的花粉被描述 (頁 403—404, 插圖 232, B—D), 这些是 *P. Sceptrum-carolinum* L., *P. flammea* L., *P. Oederi* Vahl, *P. hirsuta* L., *P. rostrata* L., *P. palustris* L., 和 *P. sylvatica* L. 在这裏面, *P. Sceptrum-carolinum* L. 是屬於代表"*Capitata* 型"的 *Eusceptrum* 亚羣的,它具有三溝的花粉粒。*P. flammea* L. 和 *P. oederi* Vahl. 兩个屬於代表"*Flammea* 型"的 *Eurhizophyllum* 亚羣的种類,也同样地具有三溝的花粉粒。其餘的四种, *P. hirsuta* L. 还是屬於 *Eurhizophyllum* 的一种, *P. rostrata* L. 屬於 *Apocladus* 羣, *P. palustris* L. 和 *P. sylvatica* L. 屬於 *Cladomania* 羣,却都具有相類似的二溝花粉粒。

按照塔赫他間的花粉進化学說(被子植物形态進化,第九章,插圖 80, 1948) 的理解,二溝的花粉粒可以有兩个來源,一个是从單溝型進化而來,而另一种則是由三溝式演化出來。現在,我們在馬先蒿屬中,三溝型的花粉,是在兩端的羣中看到,而二溝式呢,則在那些中間的羣中遇到。这一附帶的証据,也給了我的以为本屬的進化,不很可能是別的方式而只能是輳合的这个理論,以一个進一步的証明。

这裏要提到的是 *P. hirsuta* L., 虽有一个离心的花序,却也具二溝的花粉粒。为了花序的特徵,它是被放在 *Eurhizophyllum* 亚羣中了,但是它也还是可能由雜交而來,而与它相对的种類,是 *P. Lansdorffii* Fisch. 那是一个体态很相似然却有着向心花序的种類。这一种按現有証据看來,是那个同時並存着兩种"基本型式"的花冠的 *Palustres* 系的祖先。

王教授答应在 1956 年來檢視 *Pedicularis* 的花粉,看一下是否所有中間羣的种類,都具有二溝的花粉粒。希望在那个工作中找出一些有價值的事情來。

如果接受了这个假設,那麼上面所有提出的問題,都可以圓滿地歸到这一原因中去,因为虽然这些現象的確是与"基本花冠型式"相衝突的,但是它們的發現,也並非是完全混乱的,而是可以看出被某些規律所支配着的。在双齒种類的問題上,幾乎所有中間類型的羣,在其發展的某一階段上,是一定会有具齒的种類的,虽然这些生齒的情形並不完全一致。只有这些顯具"*Flammea* 型"的影响的羣,才会有多齒的、"喙齒型"(*Rhynchodonta*-type)花冠,如像 *Brachyphyllum* 羣中的 *P. lutescens* Franch., *P. lyrata* Prain, 和 *Apocladus* 羣中的 *P. gyroflexa* Vill., *P. maxicana* Zucc. 等种類。而且这些种類,与他們自己的型式的順序相符合,也是經过那个双齒的階段的,因为前兩种是双齒的 *P. stenocorys* Franch. 的繼承者,而後兩种則是兩齒的 *Comosae* 和 *Sudeticae* 系的後代。相反地,那些具有顯著的"*Capitata* 型"的影响的羣,則其种類中的花冠,僅僅涉及到一个,單独的、簡單的"双齒型"而不及其他的有齒型式,如像在 *P. hirtella* Franch., *P. striata* Pall., *P. pteridifolia* Franch., *P. rex* C. B. Clarke, *P. floribunda* Franch. 及其他很多种類中所看到的一样。

对於花的大小、花管的長短和下唇的位置等各點上,我們也可以作同样的看法。在同一 *Palustres* 系中的 *P. sylvatica* L. 和 *P. lusitanica* Link et Hoffm. 的可疑的下唇位置,与 *P. labradorica* Wirsing 的模式的"*Capitata* 型"之並存,僅僅表示了这一系的雜交的性質。相同地,是那花冠的大小,这一點,正与"*Capitata* 型"的順序相反,在 *Cyathophora* 羣中,反而变为前進的了,在最原始的 *P. rex* C. B. Clarke (圖版二十六,下) 中最小,在 *P. cyathophylloides* Limpr. f.(圖版二十六,下)和 *P. superba* Franch. (圖版二十七,上) 中適中,而在最專化了的 *P. cyathophylla* Franch. (圖版二十七,下)中为最大。这个徵候,同伸長了的花管和盔上的齒联合起來。組成与本羣中所具的一般說來屬於"*Capitata* 型"的花冠的三个背馳之點。

至於眞正雜交的例子,我必須承認我对於这方面的研究之不足。但是,麗納蒂氏所提的許多例子,我是有机会看到的。为了除了麗氏以外的晚近作者,对於本屬中有雜种的冷淡的态度,我願意选出一个为这个法國作家所述及的雜种,來作特殊的例子,这就是 *P. atrorubens* Schl. (圖版二十八,下;二十九,上),而这种雜种的材料是十分充份的。这一雜种的双親是 *P. recutita* L. (圖版二十八,上) 和 *P. incarnata* Jacq. (圖版二十九,下),前者屬於 *Rhizophyllum* 羣而後者則屬於 *Apocladus* 羣。其他區別點是前者具有离心的花序及無齒的盔,而後者則花序向心而盔部有嘴。这个雜种在各點中都屬於兩親之間,而被麗氏作如下記述:

"与 *P. recutita* L. 之別,在盔端有短而却很明顯的喙,与 *P. incarnata* Jacq. 之別,則在其嘴較短,和花色不同等等"。

在上面的述記中,缺少了一件十分重要的事情,那就是花序上的區別。*P. recutita* L., 像所有眞正的 *Rhizophyllum* 羣的种類一样,是具有顯係离心的花序,而这在 *P. incarnata* Jacq. 中,則是次序相反的。不僅如此,在前者中,花是密排成短穗狀花序,而在後者中,則花是稀疏地生長的。在雜种中,花序和其他特徵一样,是在中間型的狀态中的。花開次序很难直接称为离心,因为所有的花是幾乎同時開放的,而在疏密上,則是以接近 *P. recutita* L. 的情形为多 (圖版二十八,下),但是像 *P. incarnata* Jacq. 一个模样的情形(圖版二十九,上),也不是完全沒有。这一點对於当它是一个雜种的想法,是增加了一些重量的。

这裏是一个雜交的例子,它不單是在屬於不同羣的种類之間,而且也是在具有進化上不同階段的花冠的种類之間。这是会成为一件十分有兴趣的事,來找出这一雜种的羣体,在自然中是怎

样補充的，还是靠着長久持續不絕地在親本中進行雜交呢，还是靠着自已种子的成熟呢，还是兩者都有呢？这也会是同样地有兴趣來知道在進化路線的兩極端之間，那就是最高程度和最低程度的种類之間，或者在兩个相对的"基本花冠型式"的种類之間是否也有雜交情形的發生。如像为好幾个有名的学者所指出，在植物界的進化中，雜交恐要比一般所承認的，会起着一个更重要的作用，而按我們在本研究中所見的事实我們当然会贊成这样的一个見解的。

5. 馬先蒿屬的返整花[1]

在植物学中返整的花是一个有趣味的題目，我認为在这裏報告一个例子是適当的。*P. sylvatica* L. 是一个特別爱發生返整花的种類。曾有一个在花序頂部兩朵花連合成为一个双花的例子，为維甘得氏所觀察到而为伍史台尔氏所記載[2]。在这个例子中，兩个花並沒有表現出退化的現象來[3]，因为除了各部分的合生之外，兩个花的上唇，虽然多少有所变化，还仍然是盔狀的，而兩个下唇則为一个不知起源的，增加出來的三角形花瓣所連接。

在邱園标本室中，在同一种中，还有一个例子，在那裏面，上唇已完全退回成兩个分离的普通花冠裂片了。那个植物是一个貧乏的植株，高不達 3 厘米。在葉和萼上是看不到什麼異樣的。上面只有兩个花，而僅其中的一个在花期中。它的花管長約 18 毫米，在管頂伸張着 5 个幾乎相等的，圓卵形的花冠裂片，那兩个代表盔部的裂片是比代表下唇的要微微地小一些。这現象的有趣之點，是在於花柱和雄蕊的長度，和後者的數目。这兩种器官的長度，似乎一些也沒有受到上唇退化的影响，因为它們还都是 11 毫米長，約等於在正常花中的長度。与長度相反，雄蕊的數目，則与花冠退化相合，而增加至 5 枚了。雄蕊的花絲，一直自花管的喉部伸出，而上部有毛。其花柱則在伸出部分的中間，向下屈曲成一半环，以相合於正常花中的原來位置。这是一个与維甘得氏所報告的不同的，毫無錯誤地表示一种退化現象的例子。

6. 对於一般進化的討論

当人們談到進化時，他一定要有一个为其理論所依据的基礎，而这对於一个分類学家來說，那就得是外部形态上的特徵。但是，这些特徵的选取，是这样地因人而異，所以为一个作者所选取的，不但是可能与另一著作所选者不符，而且可能是恰恰相反的；而且，所得的結果也未必与其他植物学部門中所得的結果相印証。在这样情况之下，配与植物的各階層的系統位置，或是作为原始的，或是作为進化的，就常有受到批評的可能了；而这就是單靠形态特徵所得到的推断的唯一弱點。很幸运地，不像在別的屬中一样，在本屬中一方面相近种類的在营养器官上的相似性，另一方面在花冠構造上有定向的進步，能这样確定地、明晰地表示出一直線的進化來，使人很难找到理由來怀疑系統的安排方法。所以在本屬——作为植物界的極小的，然而却是不可分割的一部分——的可靠的進化情形的研究中，我們在一定程度上，可以粗略地想像出在怎样的情况下，古代的簡單的植被，經过了漫長的時代，而進化成为現代的無限複雜和繁多的情形。虽然这裏不是一个可以長篇地來討論种的形成問題的地方，但是我相信在本研究中所看到的，对这一細緻問題中的某些特殊方面，能多少加以闡明。

現在在种的形成方面有兩个不同的学說，一个是較老的達尔文学說，或普遍叫做達尔文主义，另一个是李森科在 1950 年發表的新学說。我們要对在本文中得到証明的各點來談談。在老

1) Peloric 这个字的意义，原來是指已然進化为左右相称的花，退回成放射相称的一种情形的，我現在試譯为"返整"，不知是否有当。

2) 伍史台尔：植物畸形学，二卷 (1916)，239，圖版 51 之 6；插圖 145,146。

3) 維尔孟：植物界的反常現象 (1926)，106 頁。

的学說中，种是由变种以逐漸的、緩慢的过程形成，变种因微小的变異的固定和累積而与其原來的類型愈去愈远，終於变成新种；正因为种的形成，是由这样的緩慢而逐漸的步調而來的，那麼除去因絕种而形成間斷外，在老种与新种之間是一定会有中間型的。在这一学說中，以生殖过剩而造成种內的生存競爭，是被認为形成新种的主要刺激素。照新的学說看來，种的形成是在一种間斷的進程之下，以突然的、飛躍式的方式实現的；因为它們的發生的突然性，故在种間是存在着進化的間断的，而在新舊种之間，是沒有中間型的。

經由我們在馬先蒿屬中的研究，这幾乎已然成为十分顯著，的確是有兩种完全不同的步驟，在本屬的進化中起着作用。其第一种是以一种均匀的，一步一步的方法進行的，而第二种則是以一种較为基本而且以飛躍或爆發的方式發生的变化來实現的。

有一种特殊的現象引起我注意的，就是在各羣及各亞羣中的花冠構造專化的規律性，例如在 *Rhizophyllum* 羣中由"無齒型"(*Anodontae*)，經由"双齒型"(*Bidentatae*)、"喙齒型"(*Rhynchodontae*) 与"長喙型"(*Longirostres*) 而達於"長管型"(*Siphonanthae*)。这裏就是代表以緩慢而均匀步調進行的第一种方法。在这一种進化中，花部器官的改变，不但是較为顯著，而且一般地是較早於营养器官的。这也很好地为 *Rhizophyllum* 羣所表示出來，在那裏面从 *Flammeae* 系至 *Macrorhynchae* 系，在後一种器官中是很少变化的，而在前一种器官，則已从"無齒型"進化到"長喙型"了(參閱圖版九、十与十一上)。類似的情形也在 *Eucyclocladus* 亞羣中自 *Salviaeflorae* 系至 *Coniferae* 系(參閱圖版十七、二十三与二十四)和 *Cyathophora* 羣中自 *Reges* 系至 *Cyathophyllae* 系 (*P. rex* C. B. Clarke 圖版二十六，上；*P. cyathophylloides* Limpr. f.，圖版二十六，下；*P. superba* Franch.，圖版二十七，上；*P. cyathophylla* Franch.，圖版二十七，下) 的整个發展線上看到。虽然在具有較長的歷史背景的羣中，与主要的花部变異相伴而來的小变動，最終也將会把在較高水平上的种類，变成很不相同的類型，然而这是非常明顯的，如果本屬祇靠这种緩慢而有規律的步驟來進化，則除了開始的兩羣——*Rhizophyllum* 与 *Sceptrum* 之外，將会發生很少的一些補充羣，來使現在的馬先蒿屬变为这样地丰富了，而在事实上，現在的補充羣，是在數目上十分繁多，在性質上更为複雜的。而且这种常規的進化方式，也同样地对於現在世界上植物界的多样性和複雜性，不能給与多少解答的。在進化的作用中，一定还另有其他重要的演化途徑，那就是上面已然涉及了的第二种進化方式。

在这一种進化中的驟然的、飛躍式的步驟，虽然大部分是以十分剧烈的方式表現出來的，更因为它的自己和本屬中所特有的，第一种变化中的連續進化階段中所表現出來的極端規律性相对照而發生隔离作用，而在这种作用之下，它的这种飛躍的性質，就被分离出來而愈覺顯明了。在这裏，一些基本性的变化，可能在某一次表現在大出於原有种類範圍以外的特徵上，如像在 *Cyathophora* 羣中的葉基和苞片之結合为杯狀体(參閱圖版二十六，二十七)，和 *Dolichomiscus* 羣中的主莖的突然的短縮或顯然消失 (參閱圖版十九) 等等，或另一次表現於在舊种中已有預兆的、然而未能被恰切地固定下來的一种特徵中，如像葉序之由互生而轉变为对生(輪生)。我們曾指出本屬中是有極大的互生葉的种類，改为对生的趨势的，这一現象在一極大數目的种類中遇見，尤其在 *Cladomania* 羣中，如 *P. lanceolata* Michx.，*P. palustris* L. (參閱圖版十二，下)、*P. resupinata* L. (subsp. *oppositifolia* Tsoong) 等种中。但是，無論这一趨势如何强烈，在互生葉序中，却沒有一个种能够眞正地、確实地得到这一徵候而加以固定下來。这一事实表示出那些確实具有对生葉的羣的出現，虽然表面上似与这个趨势有關，然而却顯然是經由一种

独特的、突然的步驟而形成的；而僅僅这一种步驟，就得出了本屬中半數以上的羣和亞羣了。

当然，这种突然的变化，在固定之後，如果得不到那个使得由此形成的种類，開始各自的独立進化路綫的第一种或常規的進化方式的支持，那麼，这些种類將会以一种奇異的、孤立的形式，生活若干時期而終趨於死亡，而不再在進化的浪潮中起何作用。像这样停止了的活動的疑似的例子，也似乎很普遍，像 *P. hirtella* Franch., *P. tsekouensis* Bonati, *P. porriginosa* Tsoong 等可举出作为例子。所以，这是这兩种不同的，但却不可分割的步驟相协調的力量，使得進化之輪，不停地运轉，像我們現在所見的一样。

在第一种緩慢的進步中，退化和舊的特徵的重現，是很容易發生的，如像在比較普遍的 *P. gracilis* Wall. subsp. *stricta* (Wall.) Tsoong 中的久已固定了的輪生葉序裏面，突然復現了 subsp. *genuina* Tsoong 的对生葉子，和在具有多齒的与原始嘴部的 *P. rhynchodonta* Franch. 的花序之中，不意地出現了“無齒型”的花等情形。不像在第一种進步中一般，在第二种突然發生的步驟中，是不会有舊徵重現的情形的。

如上所述，我們揭發了一个最有趣的事实，那就是为達尔文和李森科所指出的兩种根本不同的新种形成步驟[1)]，在植物界進化中的共存。它們不僅共存，而且它們在事実上是互相密切协調，以推進進化的。達尔文以他的在生物科学中極廣博的知識，再加以在他的極細緻的观察之下所做的大批实験，抉取了在進化中比較明顯的，也是比較普遍的一种方式，那就是第一种緩慢漸進的变化，認为係有机体前進的唯一手段，而顯然地遺漏了那第二种表現为突然的、爆發式的变化的方式，这种方式是决然要比第一种發生得稀少而且是比較难於辨認的，因为这种缺乏中間類型的情形，是很容易被歸納到緣於天然选擇作用，而使中間類型已在与更完善的類型相競賽中絕滅了的那样的緣故中去的。但是决然地，这样的解釋是不能被一概地运用到有机生命的進化中去的。原因是在原先存在的羣中的舊种和以第二种突然方式出現的新种之間，是否有連接的類型存在，是大有疑問的。这一个或多个特徵，如像使 *Cyathophora* 羣成为这样地富有特色而孤立起來的这种結合了的葉基和苞片，一定是这样突然地被獲得，以至於很自然地在新舊种之間，沒有任何的中間類型可以被遺留下來。这一點又因为对生葉的种類，缺乏互生葉的变型，而更加得到了証实。

植物的生殖器官，要比营养器官为穩定而不易起变化，是一个普遍知道的事实，而挽近更为解剖学、細胞学、及其他植物科学中的实験所証明。正与这一个普通的規律相反，在本屬中花部表示出極大的可塑性來；营养部分反而似乎比較穩定得多，而在演化中顯得很保守，正如像在上面所指出的兩个羣和一个亞羣的例子所証明的一样。这种現象發生的原由，似乎並不在於本屬在本質上与其他顯花植物有何不同，而实由於它的特殊的虫媒的繁殖系統所致。这裏由昆虫授粉而來的对於花部的刺激，其强度和直接性，要远远地超过其他对於营养器官起作用的环境条件，是幾乎毋容置疑的。这主要地表示出环境在生物進化中所起的作用，而在这裏，它們的多方面影响，不同程度地作用於不同系統的器官中，又怎样地加深了变異的分岐性。这使我們幾乎难於相信達尔文的部份地受了馬尔薩斯影响而來的这一种假定，像这裏花部的变異和進步，应該歸入於因本屬中一些种類生殖过剩而引起的生存競爭的原因之中。

相反地，在从第一种含有極細緻的分化等級的，和久已捨棄了的特徵的局部返回的例子——

---

1) 这裏所說的新种形成步驟，是僅指对於表面現象的观察， 而並不意味着我对於李森科院士學說中的新种形成的实际步驟，完全贊同。

这些表示由这一种方式中得出的种类之間的親緣關係的親密性和連續性的例子——的進化方式中，所得來的証据下，人們就不再能同意李森科氏所提議的第二种突然的方式，無例外地控制着一切生物進化的学說了。他的以为种間存在着尖銳的界劃的这一个見解，似乎是与系統学家在日常分類工作中所見到的，在种間帶有轉变的連接類型(变种)的緩慢進步的例子，更多於具有間斷的种間關係的急劇進步的例子的經驗，恰恰相反。

[未完待續]

A NEW SYSTEM FOR THE GENUS PEDICULARIS

PU-CHIU TSOONG
(*Institute of Botany, Academia Sinica*)

PREFACE

I began my study in genus *Pedicularis* in the summer of 1948 without being aware of the work on the revision of the Chinese species to have already been undertaken by Dr. H. L. Li in the Academy of Natural Sciences of Philadelphia. When the first part of his revision was brought to my notice, it had become too late to stop my work in the genus, which by then was already well advanced, as I had passed over all Chinese material available at Kew. His viewpoint certainly gave me a great revelation regarding the evolution of the genus, but still I felt somewhat unsatisfied with the arrangements in his system. Then I began to try seriously in unravelling the complexity in phylogenic relationship within the genus. This I did by first enlarging my scope of study to include all the species of the world, as I was certain that not much would be learnt in this direction if the study was limited to any particular area.

After the formation of my basic idea in the system of the genus, I further intensified my knowledge of the genus by consulting the specimens kept in the Herbarium of the Royal Botanic Gardens, Edinburgh; the Department of Botany, British Museum (Natural History); and the Muséum d'Histoire Naturelle, Paris. I came back to China in August 1950 with the manuscript of this paper, hoping to put it shipshape as soon as possible, but one pressing business after another, including my twenty months' expedition to Tibet, has retarded my effort in this direction. Not till the summer of this year that I was able to find time to go over the whole text to make some necessary corrections and additions, to arrange the text figures and plates, and to put the paper into its final form.

Now that my paper is going to press, I would like to take this opportunity in extending my thanks to those whom I was much indebted to in my study. I wish to express my deep gratitude to Sir E. J. Salisbury, Regius Keeper of the Royal Botanic Gardens, Kew; Dr. N. L. Bor, the Assistant Keeper, and to Sir. W. W. Smith, Regius Keeper of the Royal Botanic Gardens, Edinburgh; for the privilage of my free access to their respective Gardens and Herbarium. To Dr. J. Ramsbottom, the former Keeper of Botany, British Museum; to Dr. W. B. Turrill, Curator of Herbarium, Kew; to Dr. R. S. Cooper, Curator of Edinburgh Herbarium; and to Prof. H. Hubert of Museum Paris, I owe many thanks for placing their precious materials at my disposal. Here, special acknowledgement must be made to Dr. H. Smith of the Upsala Botanic Garden,

who kindly trusted me for working on his rich collections of specimens in the Family *Scrophulariaceae* in his series entitled "Plantae Sinenses". His generosity in giving me a complete set of duplicates for the Herbarium of our Institute always brings back the happy memory of our short sojourn together. In this connection, I wish also to mention Dr. G. Taylor, now Keeper of Botany in the British Museum, and express my thanks to him for the same kind of courtesy in trusting me with the exceedingly rich and interesting material of the many collections made in the Central and Eastern Himalayas, and also for his kind donation of duplicates.

I would further take the occasion to express my indebtedness to Dr. R. Fletcher of the Edinburgh Gardens, Dr. D. Chatterjee, Messrs. H. K. Airy Shaw and J. R. Sealy and other gentlemen in the staff of Kew Gardens for their ready helps and increasing regards towards my work. Lastly, I wish also to thank Mr. G. Atkinson, artist in Kew, for his help in photographic matters which certainly much facilitated my work in the present paper.

After my return to China, I have received constant and close attention from Prof. S. S. Chien, Director of our Institute, in almost every phase of work I participated, and in the publication of this paper, he has not only given continuous encouragement, but further favoured me with going through the manuscript. I hereby give my most cordial thanks to him. I would also like to express my gratitude to the Vice Directors of the Institute, Professors Y. Ling, C. C. Chang, C. Y. Wu and Mr. C. W. Chiang for their constant and untiring guidance towards my works.

My father, the late Prof. K. K. Tsoong, started me in the career as a botanist in following his steps long ago. On July 5th, 1937, I was transferred to work in the Botanical Survey of Northwest China in Wukung, Shensi Province. Two days later, on the 7th. of July, the Japanese militarists began their war of aggression in Peking, and my father was compelled to return to Ningpo, his birth place in Chekiang Province, where he fell a victim to pneumonia three years later. When I left him here in Peking seventeen years ago, I scarcely dreamt that it was the last time in my life to see him. To him, who would remain ever dearly in my memory, the following pages are affectionately dedicated.

P. C. TSOONG

Peking, China.
August, 1955.

PART ONE

INTRODUCTORIAL

I. Historical Notes

The present genus has seen much effort devoted to its studies and revisions in the past. The systems of importance are Steven's of 1823[1], Bunge's of 1841[2], '46[3], and '49[4], Bentham's of 1848[5], Maximowicz's of 1888[6], Prain's of 1890[7], Bonati's of 1910[8] and 1918[9], and Limpricht's of 1924[10]. After a lapse of over twenty years, there appear almost simultaneously but independently two works, one by a Japanese author, Mr. Isao Hurusawa[11] and the other by a Chinese botanist, Dr. H. L. Li[12].

As to the earlier systems, in spite of the fact that certain schematic reproductions are made in the latest revision of Dr. Li, it is thought advisable to repeat the process here, not merely for easier comparison without cross-reference, but also for making up certain discrepancies caused by the difference in my viewpoint from that of Dr. Li.

1. System of Steven

Tribe 1. Personatae: Leaves opposite or alternate; lower lip erect.
Tribe 2. Verticillatae: Leaves 4-verticillate; lower lip spreading.

---

1) Steven, C.: Monographia Pedicularis, in *Mém. Soc. Nat. Moscou*, VI, 1 (1823), 60, pls. 1-17.
2) Bunge, A.: Ueber eine neue Art der Gattung Pedicularis, in *Bull. Acad. St. Pétersb.*, VIII (1841), 241-253.
3) Bunge, A.: Ueber Pedicularis comosa L. und die mit ihr verwandten Arten, in *Bull. Phys.-Math. Acad. St. Pétersb.* 5 (1846), 369-384.
4) Bunge, A.: Pedicularis, in *Ledebour, Flora Ross.* III (1849), 268-303.
5) Bentham, G.: Scrophulariaceae, in *DC. Prodr. Syst. Nat. Regni Veget.* X (1846), Pedicularis, 560-582.
6) Maximowicz, C. J.: Pedicularis L., Synopsis generis nova, in *Bull. Acad. St. Pétersb.* XXXII (1888), 515-619, pls. 1-7, et in *Mél. Biol. Acad. St. Pétersb.* XII (1888), 769-919, pls. 1-7.
7) Prain, D.: The species of Pedicularis of the Indian Empire and its frontiers, in *Ann. Bot. Gard. Calc.* III (1890), 1-196, pls. 1-37, 1 map.
8) Bonati, G.: Contribution a l'étude du genre Pedicularis, in *Bull. Soc. Bot. France*, LVII (1910), Mém. 18, 1-35.
9) Bonati, G.: Le genre Pedicularis L. Morphologie, classification, distribution géographique, évolution et hybridation (1918), i-x, 1-168, 1 pl.
10) Limpricht, W.: Studien über die Gattung Pedicularis, in Fedde, *Rep. Sp. Nov.* XX (1924), 161-265, 1 map.
11) Hurusawa, S.: The genus Pedicularis, in *Journ. Jap. Bot.* XXI (1947), 159-166, XXII (1948), 11-16, 70-76, 178-184, XXIII (1949), 20-24, 106-112.
12) Li, H. L.: A Revision of the genus Pedicularis in China, pts. I et II, in *Proc. Acad. Nat. Sci. Philad.* C (1948), 205-378, pls. 15-23, CI (1949), 1-214, pls. 1-16.

Tribe 3. Faucidentates: Leaves alternate; lower lip spreading, galea dentate at base.
Tribe 4. Rostratae: Leaves alternate; lower lip spreading, galea beaked.
Tribe 5. Bicuspidatae: Leaves alternate; lower lip spreading, galea bidentate at apex.
Tribe 6. Edentulae: Leaves alternate; lower lip spreading, galea edentate at apex.

In the above system, there exists a rather interesting point, namely, the creation of a separate tribe, *Personatae*, by isolating all species possessing an apposed or erect lower lip, as opposing to all the others having ringent, or spreading lower lip—a process conspicuous by its absence in the works of most later authors. Contrary to the criticism of Bonati as "parce que son point de depart est peu natural," this point is, in fact, a most important criterion in the classification of the genus. It shows, on the part of the author, an appreciation in the existence within the genus of the two radically different types of corolla as what might be termed as "Basic corolla-types", without the separation of which, a natural system can never be attained. The reason will be fully discussed in due time.

His system, however, is not entirely satisfactory, because of the lack of a thorough understanding of the mutual relationship of those two "Basic types" of corolla. This is shown in his exclusion of certain species with obvious "Personatae" structure of corolla as *P. tristis* L., *P. acaulis* Wulf etc. from the tribe *Personatae*.

Besides the maintenance of a separate tribe for the verticillate-leaved species, the bulk of his system with tribes 3-6 has already been greatly influenced by the overwhelming evidence manifested by the development in corolla of purely evolutionary consequence, which, for the sake of a clearer conception through contrast, may be designated as "Evolutionary corolla-types" to stand against the "Basic types" alluded to above. The failure on his part in tracing the line of evolution in the respective field of the two opposing "Basic types" was perhaps due to the scantiness of species in his knowledge, thus being insufficient to show uninterruptedly the lineal relationships as the rich material does today. Consequently, his system is already in a sense more artificial than natural.

2. Systems of Bunge

Bunge deviced altogether three sets of systems. The first, published in 1841, is as follows:—

Verticillatae: Leaves verticillate or opposite.
  Sect. I. Erostres: Galea beakless.
  Sect. II. Rostratae: Galea beaked.

Sparsifoliae: Leaves alternate, very rarely opposite.

Sect. III. Tubiflorae: Flower long-tubed.
Sect. IV. Rostratae: Galea beaked.
Sect. V. Platyphyllae: Broad-leaved.
Sect. VI. Basidentatae: Galea two-toothed at base.
Sect. VII. Bidentatae: Galea two-toothed near apex.
Sect. VIII. Edentatae: Galea toothless.
Sect. IX. Macrantha: Flower large, lower lip erect.

This system is analogous to Steven's in keeping the *Verticillatae* separate. In the alternate-leaved realm, the system seems somewhat more of a mixed nature. Sect. IX *Macrantha* apparently equals in part Steven's *Personatae*, but by including in it *P. tristis* L., *P. capitata* Steven and *P. acaulis* Wulf., his better understanding in "Basic corolla-types" is well manifested. Another outstanding feature is the creation of a section free from floral characters—Sect. *Platyphyllae*, which holds species like *P. resupinata* L., *P. lanceolata* Michx., *P. bifida* Pennell (*P. carnosa* Wall.), *P. racemosa* Douglas etc., all having very congenial habit. Although all other subdivisions are still based on "Evolutionary types", this is justifiably the best system of all earlier works.

Perhaps, because of the reappearance of *Rostratae* in both Sect. II and Sect. IV or for some other reasons, he re-arranged his system in 1846 as follows:—

Sect. I. Cyclophyllum: Leaves verticillate or opposite.
Sect. II. Siphonantha: Leaves alternate, flower long-tubed.
Sect. III. Rhyncholophae: Leaves alternate, flower long-beaked.
Sect. IV. Pharyngodon: Leaves alternate, galea two-toothed near throat.
Sect. V. Lophodon: Leaves alternate, galea two-toothed near apex.
Sect. VI. Anodon: Leaves alternate, galea toothless.
Sect. VII. Macrantha: Leaves alternate, flower large, lower lip erect.

Here all verticillate-leaved species are simply united into *Cyclophyllum;* also new names are introduced to some of the sections. The Sect. *Platyphyllae* is omitted and its constituents are poured into Sect. *Rhyncholophae.*

Three years later, another system with certain alterations appeared as follows:—

A. Subgen. Pedicularis-legitimae: Lower lip spreading or porrect, not enveloping the galea.

Sect. I. Cyclophyllum.
Sect. II. Siphonantha.
Sect. III. Rhyncholophae.
Sect. IV. Pharyngodon.
Sect. V. Lophiodon.
Sect. VI. Anodon.

AA. Subgen. Sceptrum: Lower lip enveloping the galea, anther-cells obtuse.

AAA. Subgen. Diacmandra: Lower lip enveloping the galea, anther-cells long-acuminate.

Here special emphasis is laid on the length of the lower lip in contrast with the galea as to whether the former envelops the latter or not, and this furnishes, with the coordination of the shape of anther-cells, the main criterion for the subdivisions of the genus. This, in fact, is less worthy recommending than his previous system, since the length of the lower lip is of smaller importance than its position as to whether it is spreading or erect; by over-emphasizing the length, *P. Sceptrum-carolinum* L. and *P. grandiflora* Fisch. are divorced from the closely allied *P. capitata* Adams, *P. acaulis* Wulf and *P. tristis* L. whose series *Macranthae* is placed in "Anodon" under Subgen. *"Pedicularis-legitimae"*. Furthermore, as we know to-day, apiculate anther-cells occur also in *P. centranthera* Gray, *P. plicata* Franch., *P. pycnantha* Boiss., and most species of ser. *Aloenses;* it is not to be so highly esteemed as to bear subgeneric significance.

3. System of Bentham

Ser. I. Verticillatae.

1. Longirostres.
2. Brevirostres.
3. Erostres.

Ser. II. Siphonanthae.

1. Longirostres.
2. Erostres.

Ser. III. Faucidentes.

1. Longirostres.
2. Brevirostres (vel Erostres).

Ser. IV. Bicuspidatae.

1. Ramosae: Stems branched.
2. Gladiatae: Stems simple; leaves simple-pinnatipartite.
3. Comosae.: Stems simple; leaves more dissected.

Ser. V. Edentulae.

1. Foliosae: Cauline leaves well-developed; spike long, galea beakless.
2. Uncinatae: Stems elate, foliate; spike long, galea beaked.
3. Scapiformes: Stems scapiform, few-leaved or nude; spike short; galea beaked, glabrous.

4. Humiles: Stems variable, low; spike short and dense, galea beakless.

5. Tristes: Stems elate; galea beakless or short-beaked, villoso-marginate.

6. Racemosae: Stem branched; leaves crenate or rarely dissected; flowers racemose, galea beaked, rarely beakless.

7. Acaules: Stem undeveloped.

Ser. VI. Personatae.

The higher subdivisions which he designated as "series" are apparently the same as Steven's "tribes," except that the long-tubed forms are kept in a separate group "Siphonanthae". In the minor groupings which constitute the real series, the selection of criteria shows even greater inconsistency than Bunge as shown in the employment of pure floral characters under the first three "series" and the paradoxical use of vegetative habit in the fourth and fifth, a manifestation of unsettled competition for supremacy between natural and artificial arrangements. The chief value pertains, as pointed out by Prain (page 1) to the initiation in grouping closely allied species into series which later form the basis of all systems.

4. System of Maximowicz (1881)[1]

Tribe I. Longirostres: Corolla-tube cylindric, stamens inserted at the top of tube, beak normally long.

1. Siphonanthae: Leaves alternate.
2. Longirostres-verticillatae: Leaves verticillate.

Tribe II. Rhyncholophae: Corolla-tube cylindric, dilated towards the throat, galea more or less long-beaked, rarely beakless, anterior margin toothless; leaves alternate.

Tribe III. Verticillatae: Corolla variable, never long-beaked; leaves opposite or verticillate.

Tribe IV. Bidentatae: Galea with scarcely developed beak or beakless, anterior margin two-toothed near apex; leaves alternate.

Tribe V. Anodontae: Galea beakless, with entire margin and rounded front; leaves alternate.

With the exception of retaining *Verticillatae* from Bentham, Maximowicz's work sinks deeper into purely artificial arrangement, because here for the first time, the comparison between "Basic types" of corolla

1) His first system published in *Mél. Biol.* X (1877), and in *Bull. Acad. Sci. St. Pétersb.* XXIV (1877) does not differ much from the second one of 1888, and is therefore omitted.

so emphasized by Bunge and others is wholly discarded. The true merit lies, however, in the elaboration of more definite series which were initiated by the author before him, and also in his intimate knowledge of species, which are accompanied in greater part by most critical illustrations ever produced in the studies of the genus.

5. System of Prain

Division I. Longirostres: Corolla-tube straight, slender, uniform; lip large, sessile, more delicate in texture than the firm long-beaked hood.

Section 1. Siphonanthae: Corolla-tube much elongate; stamens inserted above middle of tube; leaves alternate.

Section 2. Orthorhynchae: Corolla-tube much shorter; stamens inserted near base of tube; leaves verticillate.

Division II. Aduncae: Corolla-tube curved, cylindric, slightly enlarged towards the throat; lip sessile or stipitate, more delicate in texture than the beaked or beakless hood.

Section 3. Rhyncholophae: Hood beaked or sometimes beakless.

Section 4. Bidentatae: Hood beakless or short- and broad-beaked, two-toothed below the apex.

Division III. Erostres: Corolla-tube infract, infundibuliform; lip stipitate, base erect, two-crestate above, patent, of same texture as the beakless hood.

Section 5. Anodontae: Hood erect, beakless or with short rudimentary beak, toothless or only toothed at the lower portion of margin, with rounded apex.

We see in the above system painstaking observations of corollal structures far surpassing those of the previous authors. But because of the failure in distinguishing the "Basic types" from the "Evolutionary types", his excellent effort is somewhat wasted owing to the mixing up of these two entirely different sets of characters. Plainly, it is impossible to discuss all the points here, but we may mention a few to show what our criticism means. Take, for example, the tube in relation to the insertion of stamens. In the short-tubed species, the stamens as a rule are inserted near the base of the tube, just as in long-tubed species; the insertion is always near the throat of the tube. This clearly shows that the character is evolutionary. But according to what we see in the character of stipitate lower lip, it is closely associated with the difference in "Basic corolla-types" as it is only found in one of the two "Basic types", but wholly absent in the other, and is therefore constitutional. All these we shall have much to say later on. To return to the system itself, in spite of the laborious work involved, it does not contribute very much as far as the nature of

the system is concerned. Of course, like Maximowicz, Prain's clear conception of most of the series which are greatly elaborated by him and his definite recognition of the Himalayan species are beyond criticism.

6. System of Bonati (1910)[1]

Division I. Erostres: Galea beakless.

Tribe I. Anodontae: Galea toothless.

Sect. 1. Anodontae-alternifoliae: Leaves alternate.

Sect. 2. Anodontae-verticillatae: Leaves verticillate.

Division II. Rostratae: Galea beaked.

Tribe II. Bidentatae: Corolla-tube generally dilated toward the throat, galea two-toothed below the apex.

Sect. 3. Bidentatae-alternifoliae: Leaves alternate.

Sect. 4. Bidentatae-verticillatae: Leaves opposite or verticillate.

Tribe III. Rhyncholophae: Corolla-tube dilated towards the throat, galea with entire margin.

Sect. 5. Rhyncholophae-alternifoliae: Leaves alternate.

Sect. 6. Rhyncholophae-verticillatae: Leaves opposite or verticillate.

Tribe IV. Longirostres: Corolla-tube cylindric, not dilated above, galea with entire margin.

Sect. 7. Siphonanthae: Leaves alternate.

Sect. 8. Orthorhynchae: Leaves verticillate or opposite.

With all the alterations introduced into this system, the basic idea does not receive any drastic change and the system remains much the same as Prain's. After his intensive study on hybridization of European *Pedicularis*, a new idea led him to an inaccurate yet nevertheless very interesting conclusion that forms the basis of his second system. The idea[2] is that "Anodontae" and "Bidentatae" arose from a common ancestral stock, the presumed *"Paleo-Pedicularis"*, and are thus of the same status rather than in the case of one being the derivative of the other. This *Paleo-Pedicularis* (X) first developed into two groups: the *Paleo-Erostres-alternifoliae* (X^1), and the *Paleo-Erostres-verticillatae* (X^2). From (X^1) further sprang two subgroups, *Bidentatae-alternifoliae* (CP) and *Anodontae-alternifoliae* (C'P'). From (X^2) arose *Bidentatae-verticillatae* ($C'_1P'_1$) and *Anodontae-verticillatae* (C_1P_1). Both *Alternifoliae* and *Verti-*

1) Dr. Li cites a scheme of Bonati which he takes to be the system of 1918, but, in fact, is one of 1910 which Bonati himself reproduced in a more concrete form in 1918; the new system at the end of the latter work (page 137) has, however, been completely overlooked.

2) See scheme X of Bonati, facing page 158.

cillatae of *Bidentatae* are assumed, on the ground of lack of hybridization between them and other groups, that they are remote geneologically from the higher groups, and that their activity in evolution stopped short in their respective positions. The function of floral development is supposed to have been carried on by alternate- and verticillate-leaved *Anodontae* alone which arrived at the highly specialized *Siphonanthae* and *Orthorhynchae* through *Rhyncholophae-alternifoliae* and *Hypothorhynchae* respectively.

Thus his system of 1918:

Division I.—Bidentatae.
- Sect. 1. Bidentatae-alternifoliae.
- Sect. 2. Bidentatae-verticillatae.

Division II.—Edentatae.
- Sect. 3. Anodontae-alternifoliae.
- Sect. 4. Rhyncholophae-alternifoliae. } Leaves alternate.
- Sect. 5. Siphonanthae.
- Sect. 6. Anodontae-verticillatae.
- Sect. 7. Hypothorhynchae. } Leaves verticillate.
- Sect. 8. Orthorhynchae.

On arriving at such a conclusion, a serious controversy was overlooked. On page 159, mention is clearly made that inside the puzzling group *Superbae*, *P. superba* Franch. belongs to *Hypothorhynchae* and *P. cyathophylla* Franch. to *Orthorhynche*. In 1910, Bonati placed the series, with the two-toothed corolla of *P. rex* C. B. Clarke as a basis, in *Bidentatae-verticillatae*, and clearly he had no intention to change its position in 1918. By acknowledging *P. superba* Franch. as a *Hypothorhynchae* and *P. cyathophylla* Franch. as *Orthorhynchae*, and at the same time keeping them together in *Bidentatae-verticillatae*, he has not only annihilated his own hypothesis as to the arrested evolution in *Bidentatae*, but also seriously upset the harmony of his own system.

By the evidence provided by the same group (Ser. *Superbae*, sensu latissimo), he further asserted that alternate- and opposite-leaved species belong to two parallelly evolving but quite independent groups. This is apparently in line with, and being the predecessor of, Dr. Li's idea. In spite of this, he still took, without alteration, the phyllotaxy as the basis of secondary divisions only.

7. System of Limpricht

A. Erostres.
- I. Anodontae-alternifoliae.
- II. Anodontae-verticillatae.
- III. Bidentatae-alternifoliae.
- IV. Bidentatae-verticillatae.

B. Rhynchophorae.

V. Rhyncholophae-alternifoliae.

VI. Rhyncholophae-verticillatae.

VII. Longirostres-siphonanthae.

VIII. Longirostres-orthorhynchae.

Limpricht's system is essentially the same as Bonati's of 1910, except that it is even more regularly arranged in the order of "Evolutionary types". Although the phylogenetic diagram at the end of his work shows some appreciation to the differences between the "Basic types" of corolla in directing *Salviaeflorae* in the wake of *Gloriosae*, thereby freeing it from *Verticillatae*[1], it does not prevent him from following in the steps of the previous authors, and keeping that species in "Anodontae-verticillatae" in the actual system.

8. System of Hurusawa

The system of Mr. Hurusawa (in Japanese) divides the genus by a key in Latin into two sub-genera, ten sections and a number of sub-sections. To illustrate the general idea, subdivisions included in his key are reproduced as follows:—

A. Subgen. Rhynchophorum: Hood beaked, only beakless in P. *Perrottettii* Bth.

Sect. I. Siphonanthae: Leaves alternate.
Subsect. Rhinanthoides
Subsect. Muscicolae

Sect. II. Orthorhynchae: Leaves verticillate.

Sect. III. Tibeticae: Leaves alternate.

Sect. IV. Axillares: Leaves verticillate or alternate.

Sect. V. Hypo-orthorhynchae: Leaves verticillate.

Sect. VI. Rhyncholophae: Leaves alternate.

B. Subgen. Sceptrum: Hood beakless, entire or bidentate.

Sect. VII. Hyporhyncholophae: Leaves verticillate.
Subsect. Ikomanae
Subsect. Lyratae

Sect. VIII. Metanodontae: Leaves verticillate.
Subsect. Caucasicae
Subsect. Cyclophyllae
Subsect. Moschatae

1) See phylogenetic diagrams 1 and 2 after page 400 and the map of geographical distribution.

Sect. IX. Lophiodon.
1. Subsect. Palustres: Leaves alternate.
2. Subsect. Comosae: Leaves alternate.
3. Subsect. Striatae: Leaves alternate or opposite.

Sect. X. Anodon.
4. Subsect. Acaules: Leaves alternate.
5. Subsect. Grandiflorae: Leaves alternate.
6. Subsect. Lanatae: Leaves alternate.

In the above, in spite of the reintroduction of the long-abandoned *Sceptrum* of Bunge as a subgenus, the definition as originally applied to it by its author is completely lost, as we see under it being placed groups of totally different constitution as far apart as *Lanatae* and *Moschatae* with ringent lip together with *Striatae, Acaules* and *Grandiflorae* which are true "Sceptri", in possessing apposed lower lips. Although a liberal change is made in the names of subdivisions, Mr. Harusawa's system does not differ materially from that of Limpricht, as his "Rhynchophorum" and "Sceptrum" are mere equivalents of "Rhynchophora" and "Erostres" of the previous author.

Before going on to Dr. Li's system which is on an entirely different basis, we may sum up all the past systems together. They are of two categories: the first covering the mixed systems of Steven, Bunge and Bentham; the second covering the purely artificial ones of Maximowicz, Bonati, Limpricht, and Hurusawa. In the first, some attention is paid to the divergence in the "Basic types" of corolla, but in view of the failure to trace the differences into higher realms, efforts were only made to separate the comparatively primitive forms and even this was done without definite standardization. In the second, even this meagre effort is discarded. In the systems predominently or wholly based upon "Evolutionary corolla-types", species which are on the same evolutionary stage but are phylogenetically not nearly related are kept in the same section, and it thus invariably creates in one's mind a kind of "horizontal" effect, which forms a serious barrier to a truly natural system. Not that all these authors are unaware of the phylogenetic relationship between different higher taxa, as is well shown in the discussions forwarded by them, especially by Limpricht, but that this kind of system simply makes it impossible to keep closely allied series in a lineal order. In certain cases, the floral structures and vegetative characters of a given group, under the influence of such irrational arrangement, manifest such a paradox that when the system itself is based on "Evolutionary corolla-types", there is no possibility of any harmony, irrespective of whatever position allocated to it. This is again instanced most vividly by group *Cyathophora*, which as has been pointed out by Dr. Li, is a mere equivalent of the old, all-embracing series *"Superbae"*. The species in this group share in their vegetative organs a character that makes them scarcely

associable with the species of other groups, and that is the presence of cup-like leaf-bases and bracts. On the other hand, to judge by their floral structures, in spite of their small number, they actually occupy four different stages of evolution, from "Bidentatae" to "Longirostres" (*P. cyathophylla* Franch. is not only a "Longirostres", but already an opposite-leaved "Siphonanthae"). Thanks to this peculiarity of the vegetative organ, it is so unique that all the species are united into an inseparable whole. On such an occasion, to sacrifice this character in favour of the floral structures which form the basis of the system, and to keep them separately in four different sections in concord with their respective corolla would be a procedure appearing definitely unreasonable. Reversely, if by relying on this peculiarity, they are associated arbitrarily into a single series, and then by selecting one of the four evolutionary types as basis, the series is kept in that section to which this type happens to belong; there is no doubt that the species with corolla dissimilar to the one selected will be in a paradoxical position, and that is enough to render the system a spot of gross disharmony. So, if the system is not changed, then the only alternative is to select one of the procedures, although both of them are irrational. In the above systems, without exception, the latter procedure is selected. Bonati keeps them all in "Bidentatae", although in so doing, he has experienced some degree of discomfiture, as he makes in the chapter of geographical distribution the remark "Le *P. superba*, de la série de Superbeés, dont la seriation est difficile....." (page 63, 1918). However, the contradiction shown between this particular criterion and the floral parts has not given this author enough revelation to make him realize the complete wrong footing of his system, so as to straighten out the awkward position with a thorough revision. So are the cases with Limpricht and Hurusawa, who keep series *"Superbae"* without alteration in "Bidentatae-verticillatae" and Sect. "Hyporhyncholophae" respectively.

9. System of Li

Perhaps due to the dilemma aroused from placing the old, paradoxical series *"Superbae"* and also owing to other discrepancies in the old systems, Dr. Li began to realize that the previous systems are founded on a completely wrong basis. A definite conception, that the various types of corolla as toothless, toothed, beaked and long-tubular are mere results of evolution, is formed; and if they are applied as the chief cleavage of a system, disrupted relationship will be the sure result. A revolutionary step is taken; stress is being put on phyllotaxy and general habit instead of the evolutionary steps of corollal structure. The result is that, Li's system, being diagonally opposite to all the previous ones, is no more completely "horizontal", but so to speak, "vertical" to a certain extent. Such a vertical order renders it possible to create larger natural groups (the sections in his system), wherein species of near genealogical affinity but in different

stages of evolution can be distributed into lineally arranged, successive series. To illustrate the view, we may again take the old ser. "*Superbae*", the equivalent of the present group *Cyathophora* (Sect. *Cyathophora* of Li) for example. The species on four different states of advancement in the old "series" are raised to represent four different series, and then they are arranged in the sequence of *Reges*, *Cyathophylloides*[1], *Superbae* and *Cyathophyllae* to form the new group *Cyathophora*. No process of a more elucidating nature can be deviced. Yet, apparently due to his insufficient study in morphology, he is under the same notion as Bonati, being completely overwhelmed by the all powerful evidence seen in *Cyathophora*. He regards, as Bonati, all the verticillate-leaved species as belonging to an evolutionary independent group, and, under such an impression, similarities both in floral and vegetative organs between alternate- and verticillate-leaved groups are attributed arbitrarily and inclusively to the parallelism in development. Thus displacing the "Evolutionary corolla-types", he applies the phyllotaxy as the main cleavage for his system, and the genus is accordingly divided into three major groups as follows:

Grex I. Cyclophyllum: Leaves opposite or verticillate.
Grex II. Allophyllum: Leaves alternate or opposite or both.
Grex III. Poecilophyllum: do.

To employ the phyllotaxy as the basis of a system is a process of quite questionable nature, as it infuses into the system certain "*horizontal*" feeling—a feeling quite distinct from that of the system based on "Evolutionary types", but nevertheless horizontal to a degree—by keeping closely allied species in wide-apart groups. Furthermore, I find it very hard to agree with his assumption as to the primitiveness of all verticillate-leaved groups. Regarding these points, we shall have much to say later on, as it is impossible to make clear complicated problems like this in the space here. These defects which greatly devalue his system came clearly from his failure, like most later authors, to distinguish the "Basic corolla-types" and this is well reflected in the somewhat aimless arrangement of sections and series in his phylogenic diagrams, of which there are too many instances to be cited here.

Even it is true that he has not succeeded in putting forth in concrete forms the various morphological characters that must have helped him string together some of his most important groups like "Lasioglossa" and "Rhizophyllum". However his system surely carries on a great step forward, and is by far the most natural one extant.

1) Dr. Li, in his Revision (Part 1, pages 334-335), puts ser. *Cyathophylloides* before *Reges* as the starting point of group *Cyathophora*, this being an apparently inappropriate process. This monotypic series, the flower of which possesses already a swelled, rudimentary-beaked galea and a considerably spreading lower lip (although in his illustration, the lower lip is somewhat over-ringent) is certainly more advanced than *Reges* whose species have bidentate galea and a rather erect lower lip.

II. Morphology and Evolution

A. Chief and other morphological criteria, under evolutionary viewpoint, serve as basis for the system

In the past monographic works on *Pedicularis*, the various morphological characters, almost without exception, are not looked upon as parts of an organic integrity with mutual interaction between them, and thus should be studied associately from the evolutionary point of view, but rather as isolated items to be submitted in the form of a list. Because of such a detached method, criteria other than those used as the basis for classification were prevented from being taken into systematic consideration except that each served by its individual merit to distinguish species. Yet, it is more than apparent that only by incorporating all available criteria into a system can there be hope of its being at once complete and rational. In the wake of a different approach, our discussions, instead of being in the conventional order from root to seed, will be conducted in sequence of the relative phyletic importance of the various criteria.

1. *The two "Basic corolla-types" and their fundamental differences in development*

As pointed out by Dr. Li, the genus relies its fertilization mainly upon insect-pollination; the structure of the corolla is thus induced to take steps in increasing the efficiency in this direction. The higher forms, perhaps each adapted[1] to a particular type of insect-vector with its peculiar floral structure, are interesting from pure morphological point of view, but certainly poor in systematic value, since not only their corollas have modified so much from their original pattern as beyond recognition, but also their vegetative organs are bound to be subjected to a greater or smaller degree of change in the course of evolution. In fact, such forms should not be over-evaluated as to serve functionally higher than serial ranks within any truly natural system. The right approach for a systematist is therefore to seek his main cleavage in the more archaic forms; then by following the evolutionary trend with the help of various morphological features, it is possible to form the general idea about the higher subdivisions in the genus.

---

1) Strangely enough, during my twenty months' travelling and sojourn in Tibet, only twice had I the opportunity to observe humblebees visiting two species of *Pedicularis*, one *P. lachnoglossa* Hk. f. and the other *P. globifera* Hk. f. In both cases, the insects were not occupied in nectar-gathering, but rather busied themselves in collecting pollens. It would certainly make a very interesting subject of study to observe the activities of insects if one may have the chance to stay in places profuse both in species and numbers of individuals of *Pedicularis*.

In studying the systems of the past, I was deeply impressed with the attention paid by the earlier authors to the particular type of corolla which is responsible for the creation of *Personatae* of Steven and Bentham, *Macranthae, Sceptrum* and *Diacmandra* of Bunge as against the other type in their respective systems. The association of this view-point with the later ideas of different authors, such as that of distinguishing the shape of the lower lip held by Prain (p. 8), that of teeth development held by Bonati[1], that of tube curvature held by Li[2], etc., gave rise to a definite conception of two "Basic corolla-types", which have nothing to do with and are independent of the "Evolutionary corolla types".

Though seemingly much less striking in contrast with each other than what is seen in "Evolutionary types", these two forms are nevertheless structurally so different that it is very easily discerned in most of the primitive forms even in dry state. Take, for example, two sets of specimens, namely, *P. capitata* Adams, *P. Sceptrum-carolinum* L., *P. salviaeflora* Franch, and *P. rex* C. B. Clarke for one, and *P. Oederi* Vahl. *P. foliosa* L., *P. abrotanifolia* Bieb. and *P. pilostachya* Maxim. for another, each comprising two alternate and two verticillate-leaved species. Any competent worker will not fail to observe that all the four in the first group have a straight tube and apposed (or erect) lip, while those of the second group have a tube bending abruptly forward near the apex and a lower lip spreading more or less at right angle to the tube and the galea. This is the difference that has caught the attentions of the earlier authors. For convenience' sake, the first is to be designated as "Capitata-type" and the second as "Flammea-type".

The above is but a gross definition of the two "Basic types" of corolla. A detailed scrutinization of the different parts of the corollal structures reveals other important criteria which serve to strengthen the validity of the two types proposed here. The different parts of the corolla are to be discussed separately. To facilitate the discussion, mention must first be made of the two groups which are to represent these two types of corolla. The subgroup *Eusceptrum*[3] of the group *Sceptrum* that roughly comprises ser. *Gloriosae, Tristes* (sensu stricto), *Dolichocymbae, Ingentes, Lasiophrydes, Trichoglossae, Kongboenses, Subsurrectae* etc. stands for the "Capitata-type", and subgroup *Eurhizophyllum* of group *Rhizophyllum* which is composed of the ser. *Flammeae, Pseudo-Oederianae, Rhynchodontae, Filiculae, Robustae, Macrorhynchae, Longiflorae, Megalanthae,* etc. represents the "Flammea-type". The former is

1) Cf. quotation of Bonati's remarks in the next page
2) Cf. Li's observation under ser. Verticillatae in Revision I, p. 300.
3) In the discussion of the different groups and subgroups here, readers are requested to concern themselves with the phylogenetic schima at the end of the work.

simply the series *"Tristes"* in its widest sense as perceived by most authors in the past while the latter is but an equivalent of the section *Rhizophyllum* of Dr. Li with a few series added in. Any one considerably familiar with the genus would readily appreciate the indisputable phylogenic continuity of the species within these two groups especially those on the lower levels.

Following are the discussions for the different parts of corolla:

1) Galea—of the galea, the teeth that occur in a great number of species stand certainly foremost in importance. By careful study of this character in its various forms in association with other morphological features, I was able to track down its origin that much accentuated my faith in the infallibility of the "Basic corolla-types". The complete absence in one, and the clear stages of development in the other is a fact not easily ignored.

Now, let us have a critical examination of the behaviour in the evolution of the galea in these two groups. One thing which attracted the attention of Bonati in the subgroup ***Eusceptrum*** is the direct passing from ***"Anodontae"*** to ***"Rhyncholophae"*** without any ***dentate*** form of corolla happening between these two stages. In page 97 (1918), he expresses:

"Les Anodonteés, au contraire, ont naissance aux *Rhyncholopheés, et* ceci n'est pas une simple hypothese, mais un fait; il suffit pour s'en convaincre d'examiner certaines series naturelles comme *Resupineés* et les *Tristes;* nous constaterons, chez ces dernieres surtout, l'existence de tous les intermediaires, depuis la casque sans bec et ferme a l'avant du *P. tristis* L. jusqu'au bec allonge des *P. ingens* Maxim., *P. lasiophrys* Max., *cinerescens* Franch. en passant par les éspece a casque naviculaire, comme les *P. Prainiana* Maxim., *P. princeps* Bur. et Franch.

His assertion with regard to the two series, *Resupinatae* and *Tristes,* given by him to illustrate his view, is only partly true to facts, as it is apparently not a universal rule that all "Rhyncholophae" emerged directly from toothless forms, but some of them certainly came from toothed ones, as we have now ample evidence that *Resupinatae* has evolved from *Palustres,* a series almost exclusively composed of bidentate forms. But in regard to *Tristes,* his view is accurate. To present the same view in a more concrete form, it may be best accomplished by the collocation of various types of corollas in successive stages of development within the group. After *P. tristis* L. (var. *macrantha* Maxim.: Text fig. I, A, in page 82) with beakless galea, comes to the stage with the appearance of a deünite though rather rudimentary beak in *P. dolichocymba* H.-M. (Text fig. I, B in page 82), which is in turn followed by long-beaked species as *P. trichogiossa* Hk. f. and P. *Vialii* Franch. (Text fig. I, C, D in page 82). The development clearly does not involve a dentate stage in the whole process of beak-growing.

In vivid contrast with the above, the most prominent feature in subgroup *Eurhizophyllum* is the various stages of dentate galea. In *P. Oederi* Vahl (Text fig. II, A in page 83), the shape of galea scarcely manifests any difference from that of *P. tristis*. In the second stage, angulate tips show up in *P. pseudoversicolor* H.-M., which represents a prelude to the appearance of a true bidentate galea in *P. habachanensis* Bonati (Text fig. II, B in page 83). The most important step of all, however, pertains to that of *P. rhynchodonta* Franch. (Text fig. II, C in page 83), wherein, besides the presence of the main pair of teeth, there are, in addition, a few accessory, much smaller ones on the already more or less elongated beak. In the next stage, in *P. filicula* Franch. (Text fig. II, D in page 83), the elongation of the beak carries a step farther and the teeth are now in a subdued state by the missing of the main pair and the retention of the accessory ones so that the apex of the beak looks premorse. In the subsequent stages, as in *P. Wallichii* Hk. f. (Text fig. II, E in page 83), *P. robusta* Hk. f. etc., the species manifest the trait of dentate galea in having strongly two-cleft beaks that become a predominant feature in most of the higher series of the group, as evidenced by *P. Klotzschii* Hurus., *P. Fletcherii* Tsoong, *P. Scullyana* Prain (Text fig. II, F in page 83), and *P. megalantha* Don (Text fig. II, G in page 83).

From the above, it will be seen how exact are the two "Basic types" in the matter of tooth-growing. Likewise, in respect of beak-issuance, there is marked difference in the general shape-changing and in corresponding angles assumed by the various parts of the galea in the two "types". As illustrated in the text-figures, the peculiar swelling of the anther-bearing part in *P. tristis* L. and the succeeding step of the queer-looking, boat-shaped structure in *P. dolichocymba* H.-M., *P. Dunniana* Bonati, etc. as seen in *Sceptrum* are stages never found in *Rhizophyllum*. Correspondingly, the relative angles of the tube, the vertical portion, the anther-bearing part and the beak itself are much different one from the other.

Another important feature somehow related to the teeth is the crest of the galea. This secondary outgrowth of the galea, the function of which is yet unknown to us, is just as partial as the teeth themselves; in fact, they are only found in *Rhizophyllum* and those groups which manifest a certain amount of definite relationship to it. The frequency of occurrence seems to be in direct proportion to the proximity of this relationship. It, of course, occurs most readily and attains its highest development in the group itself; crested forms of the species of ser. *Longiflorae* and *Pumilliones* as *P. siphonantha* var. *birmanica* Bonati, *P. cranolopha* var. *longicornuta* Prain, *P. decorissima* Diels, *P. Garnieri* Bonati, *P. bella* var. *crestifrons* Tsoong etc. etc., are the most prominent examples. In the slightly remoter realm, there are *P. Franchetiana* Maxim., *P. insignis* Bonati, etc. In opposite-leaved groups, we find *P.*

meteororhyncha Li and *P. cristatella* Pennell et Li, etc. Contrarily, not a single instance in the development of such an accessory organ is found in the "Capitata-type" proper. Even in group *Dolichomiscus,* which begins with ser. *Acaules* having a "Capitata-type" of corolla, no trace of such a tendency is ever shown by the higher forms like *P. batangensis* Franch., *P. macrosiphon* Franch., *P. muscicola* Maxim. etc., in spite of the fact that in general habit and in respect of length of tube, these species are notoriously similar to those of the ser. *Longiflorae.*

One of the well-known features which serves to bind together the components of Dr. Li's sect. *Lasioglossa,* a mere equivalent of ser. *Tristes* of Bentham with addition of a few allied series, is the long, multicellular trichomes ciliate along the anterior margin of the galea (*vide* text figure I). This "fringe" is present in most species of the group *Sceptrum* as I now call it, and is also found in the group *Dolichomiscus* in the European *P. acaulis* Wulf. No such trait is ever found on the "Flammea" side except the hairy galea in *P. foliosa* L., *P. decorissima* Diels etc., but in the latter, the hairs, spreading all over the galea, are apparently of very different nature and most probably are also very different in function from the "fringes" in question; in the latter, it may be used as a means to prevent waste of pollens by their spontaneous dislodging, while in the former, the use is probably limited solely to the protection of flower buds against any sudden change in weather before expanding.

2) Lower lip.—Besides the respective critical positions assumed by the two "Basic types" in the lower lip as already pointed out before, some difference in size is also noticeable. In close correlation to the general size of the flowers which we shall discuss presently, the size of lower lip is generally regressive in group *Sceptrum* as it ends in its highest level in *P. excelsa* Hk. f., *P. Vialii* Franch, and *P. recurva* Maxim., all of which have a much smaller lip than those species in the beginning of the group. In group *Rhizophyllum,* it is, on the contrary, progressive as the lip becomes bigger and bigger until reaching its highest development in *P. megalantha* Don and its allies wherein the lips are so enormously enlarged as to envelop completely the galea.

As to the shape of the lower lip, each of the "Basic types" also retains certain peculiarities for itself (*vide* Text figs. I & II in pp. 82 & 83). On the "Flammea" side, the lip is always fuller in shape, being more rounded at the back and always sessile. In the higher forms, the base is often deeply cordate, as the large, auriculate lateral lobes not only spread backwards passing the side of the tube, but ultimately go over the central dorsal line of the galea so as to overlap each other behind it. At the highest level, we find in *P. megalochila* Li, *P. Scullyana* Prain, *P. megalantha* Don etc. lips which tend to become somewhat saccate, simulating those of *Calceolaria* in shape, this being a trait never found in its opponent type. On the other hand, the long-cuneate base with sometimes

narrow acute lobes as in *P. angustiloba* Tsoong, *P. kongboensis* Tsoong (Text fig. III, B in page 85) etc. of group *Sceptrum* never seems once to occur in *Rhizophyllum*. This character is further carried to the extreme in *P. lasiophrys* Maxim. (Text fig. III, A in page 85) and especially in *P. tsekouensis* Bonati (Text fig. III, C in page 85); in the latter species, the lip is long stipitate and terminates in three lobes in a most peculiar manner.

3) Tube—As found in the definition of the two "Basic types", the tube of the "Capitata-type" is given as straight and that of the "Flammea-type" as bending near the apex. Further explanation is needed to have a clear conception as regards this point. The curvature of the tube in the latter type seems to increase with the duration of anthesis, so one often sees the tube of withering corolla that clings to the growing capsule deflected so strongly that the galea literally points downward instead of assuming an ascending position (incidentally, the lingering corolla is also a trait peculiar to this type of flowers). In the former type, the tube as a rule is straight as previously defined. But should there be any tendency to curve, then it is at or near the base rather than near the apex of the tube and always inside the calyx-tube. This is very well illustrated by *P. trichoglossa* Hk. f. (*vide* text fig. 1, C in page 82), *P. recurva* Maxim., *P. proboscidea* Stev. etc. This is one of the strong contrasts between the two "Basic types", and also the only one that has drawn the partial attention of Dr. Li with the consequent separation of his section *Orthosiphonia* from *Sigmantha*, although he has missed the initial diverging point of the two.

Because of the different mechanism in the lower lips of the two "Basic types", the tubes, in evolution, also manifest certain differences in behaviour. On the "Flammea" side, the tubes merely straighten out and elongate so that the gauge of their entire length is uniform or nearly so throughout. On the "Capitata" side, owing to the erect position of the lower lip, the tubes have to subject themselves to a preliminary step of general expansion towards the throat so as to bring the lip into a horizontal plane, and the tubes become therefore more or less infundibuliform. This is very prominent in species as *P. acaulis* Wulf and *P. tsekouensis* Bonati (*vide* text fig. III, C in page 85), which represent the stage in the first expansion of the lower lip in this particular type.

Another important contrast between the two "Basic corolla-types" is in the twist of the floral parts. In the "Capitata-type", the tortuosity happens strictly in the tube itself, as can be observed quite readily in the disposition of the veins of the tubes in all the species belonging to this type (*vide* Text fig. I in page 82). Such a twist renders the upper part of the corolla, including both the lower lip and the galea, to become "resupinate" in certain higher forms. On the other hand, such tortuosity is wholly absent in the tubes of those species belonging to the "Flammea-

type". The twist, if present, exists, as a rule, only at the base of the galea, above the level of the lower lip, and the contortion thus obtained naturally involves the twist of the galea only.

As to the length of the tube, it is definitely the "Flammea-type" (represented by *Rhizophyllum*) that has evolved into this particular morphological attainment. On its opposing type (represented by *Sceptrum*), not only the slow in. improving, new world subgroup *Brevilabium* comes merely to the initiating stage of "Rhyncholophae" at present (*P. siifolia* Rydb. and *P. Canbyi* Gray), but even in the old world *Eusceptrum*, only a higher degree of beak-lengthening is reached without having the tubes elongated to any accountable length. It is almost certainly the inherent inability in tube-lengthening rather than anything else that accounts for the lack of such a trait in *Sceptrum* proper, and there is strong doubt if ever such a feature will be achieved in the age to come, as it is perhaps intimately related to the general regressive floral sizes and the twisting of the tube—steps which are probably unfavourable to the acquisition of a long tube.

4) General sizes of corollas—The sizes of corollas are in strong contrast between the two "Basic corolla-types". Among the species of earlier creation on the "Capitata" side, the sizes are generally much bigger, while in similar species on the "Flammea" side, it is just to the contrary. To wit, we have *P. Sceptrum-carolinum* Linn., *P. grandiflora* Fisch., *P. tristis* Linn. and *P. striata* Pall. for the former and *P. flammea* Linn., *P. Oederi* Vahl, *P. hirsuta* Linn. and *P. lanata* Cham. et Schl. for the latter.

In advancing, there is also manifest divergence (*vide* Text figs I, II, in pp.82 & 83) in respect to these two types. The former is in average on the decrease, as the higher the form is, the smaller the flowers become, as observed in the order of *P. tristis* L., *P. dolichocymba* H.-M., *P. trichoglossa* Hk. f., *P. lasiophrys* Maxim. and *P. Vialii* Franch. In the latter type, it is on the increase as shown by species in the sequence of *P. Oederi* Vahl, *P. rhynchodonta* Franch., *P. filicula* Maxim., *P. robusta* Hk. f., *P. Klotzschii* Hurus. (*P. macrantha* Klotz.) and *P. megalantha* Don in general.

2. *Other morphological features in corroboration of "Basic corolla-types"*

After sufficient cognizance of the two "Basic types" of corolla, we, by observing various other characters under such a light, begin to appreciate features which otherwise mean very little to a systematist. In sequence of their importance, these features are to be discussed in detail.

1) Inflorescence—The inflorescence of *Pedicularis* is mostly indefinite, viz. centripetal, but in one particular group, namely, grex *Rhizophyllum*, the representative of the "Flammea-type", it is definite, viz. centrifugal. The flowers open in a spiral order from or near the

apex downwards, and invariably, in the more typical forms, the upper half is in full bloom while the lower portion is completely in bud; or in the later stage of anthesis, the upper in fruit and the lower in flower. It is very showy in the lowly *P. flammea* L. and *P. Oederi* Vahl, and is even more so in the lofty *P. elephantoides* Benth. and *P. bicornuta* Klotz. (Pl. VII, above, below). In the less typical form as those species of ser. *Pumilliones*, in which the plants are almost in an acaulescent state, a critical examination would reveal the fact that the capsules at the centre of the rossette often ripen first and are hence larger and better developed than those situated in the outer rings which are, as a rule, insufficiently matured, this being the sure sign of a definite inflorescence.

Reversely, there is not the slightest doubt as to the order of anthesis in group *Sceptrum*, the representative on the "Capitata" side.

There exist also certain divergences in the shape of floral leaves or bracts of the two "Basic types". The highly specialized, broad-ovate, often subentire and densely imbricate bracts are the usual order of the group *Sceptrum*, while those of group *Rhizophyllum* are ordinarily foliaceous and insignificant.

2) Habit and stem—Within the Arctic Circle, the most probable birth-place of the genus, we find in existence about nine species with "Anodonta" type of corolla; they are *P. flammea* L., *P. Oederi* Vahl, *P. hirsuta* L., *P. lanata* Cham. et Schl., *P. Langsdorffii* Fisch., *P. capitata* Adams, *P. Sceptrum-carolinum* L., *P. verticillata* L. and *P. amoena* Adams. Of the nine, the last two with a corolla-tube strongly curved near the base cannot be regarded as primitive forms; the reason for so-doing will be discussed fully later on. This leaves us seven species in all, which can be divided into two groups, one consisting of *P. capitata* Adams and *P. Sceptrum-carolinum* L. and the other, all the remaining species.

In the first group, we find in *P. capitata* Adams (Pl. VIII, above) a short but well marked stem, almost naked and scapiform, or only sparingly leafy. In *P. Sceptrum-carolinum* L., the stem is not only well-developed but also not infrequently branched above.

In the second group, one striking feature common to most species is the pre-eminence of inflorescence which usually occupies the better part of the stem, coming down sometimes nearly to the very base of the plants. In evolution, this habit is strictly adhered to in group *Rhizophyllum* from beginning to the medium level (*Rhyncholophae*) as ser. *Flammeae* (*P. Oederi* vahl, Pl. VIII, below), *Pseudo-Oederianae* (*P. pseudoversicolor* H.-M., Pl. IX, above and *P. habachanensis* Bonati, Pl. IX, below), *Rhynchodontae* (*P. rhynchodonta* Franch., Pl. X, above), Filiculae (*P. filicula* Franch., Pl. X, below) and *Macrorhynchae* (*P. macrorhyncha* Li, Pl. XI, above), and to a lesser degree in the higher level (*Siphonanthae*) as species of ser. *Longiflorae, Macranthae* etc.; those especially marked

in this respect are *P. elephantoides* Benth. and *P. bicornuta* Klotz. (*vide* Pl. VII, above & below) of ser. *Megalanthae,* already mentioned before in regard to inflorescence.

The question of ramification of stem (that applies only to the condition in which the stem is branched in the upper part) is incidently a point of profound interest in the morphological point of view. In the course of my study, it becomes more and more evident that this character and the lignification of stems retain in most cases a close connection between themselves, and are, in turn, intimately associated with the duration of life cycle of the species. It will easily be seen that the species with one or both of these characters are those which are actually, or tend to be, monocarpic. To apply this to the two representative groups, the different attainment in these respects supplies good materials for consideration. In group *Rhizophyllum,* from *Flammeae* to *Macrorhynchae,* the stems are maintained in a strictly herbaceous state, never found to branch below, let alone ramified above. It is not until the group reached its highest development that annual species with stem somewhat lignified begin to occur as what is observed in ser. *Pumilliones* and *Magalanthae.*

On the reverse side, a highly ramified condition is found almost right at the starting point of the group *Sceptrum* wherein members of ser. *Gloriosae* (*P. gloriosa* Bisset et Moore, Pl. XI, below) and *Rudes* (*P. princeps* Bur. et Fr., Pl. XII, above) are good examples.

3) Leaves—In the vernation of the leaves, the two representative groups retain between them some marked differences as far as can be judged from dry specimens. In group *Sceptrum,* it is revolute, and the lobes or pinnae are on the same plane as the leaf-blade itself. In *Rhizophyllum,* in the less highly evolved species at least, the vernation is circinate—a trait quite reminiscent of the unfolding fern-fronds. Perhaps due to this particular vernation, the lobes or pinnae are set in a plane vertical in relation to the blade itself and are folded one against the other in a gill-like arrangement before or even sometimes after unfolding. Since this characteristic disposition seems to diminish gradually as the species of the group become more and more advanced, and these differences have so far been observed only in dry materials, careful verifications on fresh material are highly desirable in the future field works.

3. *Phyllotaxy vs. "Basic corolla-types" as the chief cleavage for the system*

In incorporating his idea into his system, the first of the three groups[1] in Dr. Li's Revision, the "Cyclophyllum", consisting of purely opposite

1) Here readers are reminded of the difference in meaning of the word "grex" or "group" between that applied by Dr. Li and myself. In his meaning, it apparently stands for the rank of subgenus; in mine, it is only treated in the rank of section.

(verticillate)-leaved species is considered not only as an independent group, but also as the most primitive of the three. To establish his thesis, he gives reasons which are here quoted: "In *Scrophulariaceae* in general, opposite leaves often occur in groups, that on other evidence, appear to be more primitive (also the first leaves, cotyledons, of all *Dicotyledons* are always opposite). Thus, opposite-leaved species are to be considered as more primitive than the alternate-leaved ones. The verticillate-leaved condition is found exclusively developed only in obviously ancient genera. . . ."

Dr. Li's conclusion as to the primitiveness of verticillate phyllotaxy is apparently governed more by general conception than by actual discrimination of facts. In the first place, the reason given in brackets means but very little. There are too many phenomena of retrogressions and recurrences in the evolution of plant-kingdom to make evidence of such a remote nature more than unrealistic. Families as *Caprifoliaceae, Labiatae, Acanthaceae,* being high up in the *Dicotyledons* are exclusively or predominently opposite-leaved. Of course, there are instances contrary to this as what we see in *Compositae,* wherein genera with opposite or subopposite phyllotaxy seem to be more primitive, as in *Eclipta, Eupatorium* and *Helianthus,* but this by no means gives the theory any substantial support; in fact, the question has to be considered separately in each individual case.

Secondly, his statement that in *Scrophulariaceae,* opposite leaves often occur in more primitive groups seems to me in precise contradiction to facts. For the elucidation of this important point, let us turn our attention to the family for more direct evidences.

The first concern should be the origin of the family. There are two families to which the *Scrophulariaceae* is closely related, i. e. *Convolvulaceae* to which certain species of *Kickxia* (Linaria p.p.) are extremely similar in habit, and *Solanaceae* which bears relationship to *Verbascum, Sopurbia* etc. These two families coincidently have in both almost exclusively alternate phyllotaxy. That makes it most improbable that *Scrophulariaceae* being the possible derivative from these families, should start from opposite (verticillate) phyllotaxy.

Let us see how phyllotaxy stands within the family. In Genera Plantarum, Bentham and Hooker gave diagnosis as "Folia in paucis generibus omnia alterna, in plerisque inferiora vel omnia opposita vel verticillata, summis florisque saepius alternis".

A very good diagnosis is the above, for it depicts all three forms of phyllotaxy within the family, the alternate, the opposite (verticillate) and most important of all, the strange combination of the two, viz. opposite below and alternate above—an arrangement most popular amongst the higher forms of the family.

There is little doubt that the family began with alternate-leaved genera like *Leucophyllum, Aptosimum, Verbascum* etc. in which little

specialization in corolla is in evidence. Opposite phyllotaxy, first noticed in *Calceolaria*, marks the more obvious change in floral symmetry by accompanying a strongly zygomorphic corolla with a highly improved lower lip. Hereafter, the opposite becomes more and more eminent in the higher domain of the family and the alternate occurs only sporadically here and there in rare instances; its position is being taken over by what might be called an "admixture" of the two—the strange arrangement already referred to above. All these indicate unmistakably that opposite phyllotaxy in *Scrophulariaceae* is improved from alternate, rather than vice versa, and the odd arrangement so conspicuous within the family denotes either an improved condition of the alternate-, or less probably, a degenerate state of opposite-phyllotaxy.

Our attention may now be turned back to the genus itself. One striking feature of coincidence in phyllotaxy between the family and the genus is the existence of all three arrangements, the alternate, the opposite and the odd alternate-opposite combination. Being in the predominent sphere of opposite phyllotaxy in Tribe *Euphraceae*, the true alternate-leaved species occupy, in fact, a small minority of the whole population of the genus. Within the generally accepted species of alternate phyllotaxy, a strong, inherent tendency to change into opposite is in ample evidence. Innumerable examples can be cited in its proof. In the North American *P. lanceolata* Michx., for instance, the genuine alternate state becomes almost a rarity rather than a rule, since most specimens seen are at least opposite-leaved, not infrequently also opposite-flowered (*P. lanceolata*, it should be noted, was classified as an opposite-leaved species by the first monographer). Also among the materials of *P. palustris* L. (var. *Wlassowiana* Bunge, Pl. XII, below) and *P. sylvatica* L., pseudo-verticillate branches and leaves are by no means unusual. As in the case of *P. resupinata* L. and its close ally *P. yezoensis* Maxim., opposite-leaved forms are common-place; subsp. *oppositifolia* (Miq.) Tsoong of the former serves as a good representative. Again, a comparison of the opposite *P. rigida* Franch. (Pl. XIII, above) and its ally *P. comptoniaefolia* Franch. (Pl. XIII, below), both having rather stiff and branching habit, nigrescent drying-colour, lanceolate, shallowly lobulate to subentire leaves with abundant calosity, showily bracteate and compact inflorescence, obtusely few-toothed and cleft calyx and fairly straight corolla-tube, with the alternate species like *P. corymbosa* Prain (Pl. XIV, above), *P. nigra* Vaniot (Pl. XIV, below) etc. would reveal that the former are very much the same as the latter in most respects, save, of course, the difference in phyllotaxy. It is sufficient to convince any one that their similarity is due to real phylogenic relationship rather than the result of any chancy parallelism in development. In much the same state are *P. salicifolia* Bonati vs. *P. nigra* Vnt., *P. Mairei* Bonati (Pl. XV, above) vs. *P. palustris* L., (*vide* Pl. XII, below) *P. verticillata* L. (subsp. *latisecta* Tsoong, Pl. XV, below) vs.

P. sylvatica L., *P. labradorica* Wirsing, *P. canadensis* L. (Pl. XVI, above) etc.; the calyx and the capsule of *P. verticillata* L. being extremely near those of the last three species. Their mutual relationship is rather similar to that between *P. resupinata* L. and its various opposite-leaved forms and allies. These instances not only aptly prove the fallacy of the supposition as to the independent evolution of groups in different phyllotaxy, but at the same time illustrate in no uncertain terms that the opposite-leaved races are improved from the alternate-leaved ones.

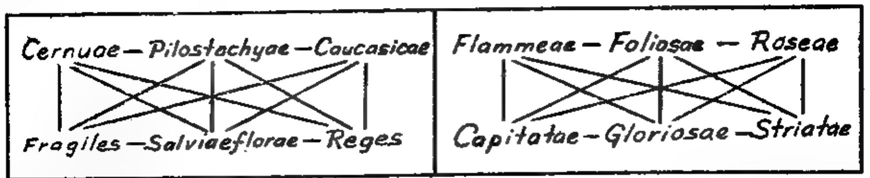
In the past, in seeing the overwhelming majority of verticillate-leaved species over the opposite-leaved ones, people simply deemed the latter to be subordinate to the former, without being aware that the latter are in most cases actually direct forerunners of the former; and there is ample testimony to prove it. Almost half of the groups of "Cyclophyllum" begins with opposite leaves, as within each group, the opposite-leaved species are invariably more primitive. Thus the initiating series of various groups and subgroups as *Salviaeflorae, Fragiles,* and *Aloenses* of *Cyclocladus,* ser. *Lyratae* of *Eubrachyphyllum,* ser. *Salicifoliae* of *Rigiocaulus* and ser. *Cernuae* of *Eudolichophyllum* are wholly or partly opposite-leaved. It will be seen that at the respective side of the two "Basic corolla-types". the groups which begin with opposite-leaved series are far closer in relationship to their alternate-leaved progenitors than those starting with verticillate-leaved series. Therefore, *Dolichophyllum* is nearer to *Rhizophyllum* by initiating with ser. *Cernuae* (*P. cernua* Bonati, Pl. XVI, below) which is furnished with a centrifugal inflorescence than *Orthosiphonia* whose starting ser. *Caucasicae* has the inflorescence centripetal. Likewise, ser. *Salviaeflorae* (*P. salviaeflora* Franch., Pl. XVII, above), which leads group *Cyclocladus,* shows a greater intimacy with *Gloriosae* (*vide* Pl. XI, below) than ser. *Reges* of group *Cyathophora* by possessing a bigger, anodontous corolla and loosely opposite branches. Also there is definite trace in the changing of phyllotaxy from opposite to verticillate. There is little doubt regarding the proximity in kinship between *P. salviaeflora* Franch. and *P. floribunda* Franch. (Pl. XVII, below), yet, the former is opposite-leaved while the latter has improved in gaining a definite verticillate phyllotaxy. In certain species, both opposite and ternate leaves are in evidence, as is instanced by *P. verbenaefolia* Franch. In its close ally *P. Smithiana* Bonati, however, the leaves are wholly verticillate. In the series closer to "Flammea-type" as *Caucasicae* and *Cernuae,* a strange phenomenon is seen in *P. sarawschanica* Maxim.[1] and *P. cernua* Bonati. Herein, both the opposite and verticillate conditions co-exist in the same individual, i. e. leaves opposite and flowers verticillate. To the best of my knowledge, there is no more suitable explanation than that the centrifugal inflorescence of the

1) *P. sarawschanica* Maxim. was originally treated as an alternate-leaved species by its author, but after a consultation of the type specimens, it turns out to be an opposite-leaved one.

"Flammea-type" origin has influenced the change of phyllotaxy to take place in the reverse order, thus it is the bracts and the flowers rather than the leaves that have been changed first into verticillate arrangement.

Enough has been said to clarify the point in issue. Now let us see what actual difference exists between the system based on phyllotaxy and that based on "Basic corolla-types". In assuming that the verticillate- and the alternate-leaved groups had evolved independently, it looks as if Dr. Li takes to the opinion that the relative phylogenetic relationships between the Capitata-typed *Salviaeflorae, Fragiles, Pentagonae, Reges* etc. and the Flammea-typed ser. *Cernuae, Pilostachyae, Abrotanifoliae, Caucasicae* etc. within the opposite (verticillate) sphere are far more intimate than those between the four former series and the same Capitata-typed but alternate-leaved ser. *Gloriosae, Capitatae, Striatae* etc., or between the four latter series and the same Flammea-typed but alternate-leaved ser. *Flammeae, Roseae, Foliosae* etc. Such arrangement only makes the closely related taxa to divorce from each other and at the same time those with rather remote relationship to stick together arbitrarily. See the following diagram:

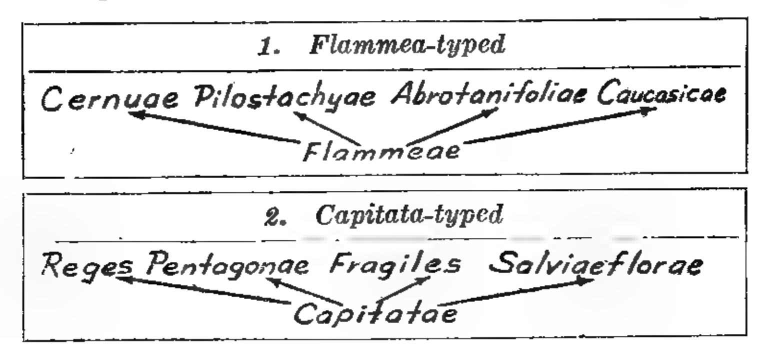
Diagram A. Classification based on phyllotaxy.



It would be extremely difficult to give any rational answer if a question is posed to the author of such a system as to whether series of "Flammea-type" had given birth to those of "Capitata-type" or vice versa, both in the opposite-(verticillate) leaved and alternate-leaved domains. Also in this connection is the difficulty arising from the disposition of the opposite-leaved forms of any alternate-leaved species as *P. resupinata* L. subsp. *oppositifolia* (Miq.) Tsoong, a form conspicuous by its absence in Dr. Li's Revision.

In contrast with the foregoing, let us see the following:

Diagram B. Classification based on "Basic corolla-types".



The above diagram gives an explicit idea to the interrelationships between the respective alternate- and opposite-leaved series pertaining to these two "Basic corolla-types". It is superfluous to emphasize here how truly each sticks to its respective type of structure during the process of changing the phyllotaxy. In addition, it is also quite perceivable how well the vegetative characters correlate in certain respects with the floral structures. On the one hand, the elate, loosely branching stems of the species of ser. *Gloriosae* (*vide* Pl. XI, below) bear mute witness to the proximity of their kinship with those of *Salviaeflorae* (*vide* Pl. XVII, above) and *Fragiles;* on the other, the characteristic short stems of *Flammeae* (*P. Alberti* Regel, Pl. XVIII, above; see also Pl. IX, X) with eminent and compact inflorescence point unmistakably to its counter-parts in *Caucasicae* (*P. pycnantha* Boiss. subsp. *tenuisecta* Tsoong, Pl. XVIII, below) and *Cernuae;* the latter further enhances the effect by bearing a somewhat centrifugal inflorescence.

The real difference of importance between the present system and all the previous ones, irrespective of whether they are based on "Evolutionary corolla-types" or phyllotaxy, lies in that, it is the actual material available to-day that we are dealing with, a purpose every botanist should strive to achieve. Instead of resorting to the imaginary, non-existent "Paleopedicularis", "Paleoanodontae" etc. as the starting points of different groups as what Bonati has done, we can point out with some certainty that *P. flammea* L. and *P. capitata* Adams are at least the existing oldest species of their respective groups, if not actually constituting the prototypes of, or even themselves be, the most primordial forms of the genus.

Besides, it becomes more logical to keep the opposite-leaved varieties in an alternate-leaved group, since they are regarded as forms not yet sufficiently established in opposite phyllotaxy, and their true opposite-leaved cousins will be found in the immediate neighbouring group instead of being in a remote sphere supposed to have no affinity whatever to themselves.

B. Other important points in the evolution of the genus

In the foregoing discussions, we have concerned ourselves chiefly about the distinction between the two "Basic types" of corolla, and the correlations manifested by other organs to the corollal. Here we are going to see, in general, the evolution of the genus wherein have been observed certain peculiarities in development, and also a number of cases which are contradictory to the "Basic types" as above defined. These can be forwarded under the following categories:

1. *Peculiar developmental behaviours.*

Within the genus, peculiar developmental behaviours often occur. A few of these are vitally connected with the establishment and disposition

of certain higher subdivisions, and thus need further explanation. The two major items are as follows:

1) Stem—We have roughly discussed before the positive evolution of the stem as indicated by its lignification and ramification. Here attention will be paid to the negative side of the picture. Most of the previous authors took to the view that *Acaules*, as its name implies, constitutes the primitive stock from which all caulescent forms of the genus were derived. There are two main objections to such a supposition. Firstly, in the face of the floral structures, viz. the already well-spreading lower lip with the corresponding enlargement in the throat of the tube, it is decidedly more advanced than the species of ser. *Capitatae* and *Gloriosae*. Secondly, like the latter series, it doubtlessly belongs to the Intermediate-temperate Flora as its geographical distribution clearly shows. As previously discussed, there are only two kinds of stems in the truly archaic forms within the Arctic Circle, we have good reason to regard therefore the acaulescent condition with suppressed main stem functionally supplanted by the abnormally elongated pedicels as an indication of improvement rather than primitiveness, since not only the same phenomenon appears repeatedly in many cases with the most prominent examples in *P. decorissima* Diels (*vide* Pl. XXII, below), but it actually proves the fact by developing into a special group, *Dolichomiscus* (Sect. *Dolichomiscus* Li, p.p.). After *P. Artselaeri* Maxim., the Asiatic counterpart of the European *P. acaulis* Wulf (Pl. XIX, above), *P. vagans* Franch. (Pl. XIX, below), the sole species of ser. *Vagantes*, takes the first step in producing long trailing shoots with axillary flowers which later become the prevalent feature in the next ser. *Longipedes* (*P. filicifolia* Hemsl., Pl. XX, above) while still retaining the telltale characteristic of the preceeding series in the long-pedicellate basal flowers. This intermediate stage is soon replaced by another in which the flowers are all born axillarilly on long shoots with the complete cessation to the basal flowers as seen in *Longipedes*, *Batangenses* (*P. batangensis* Bur. et Franch., Pl. XX, below) and *Muscicolae*.

2) Corolla—In the past, the species of ser. *Verticillatae* was often regarded as most primitive of all the opposite-leaved forms and thus becomes an involuntary stock of the so-called "Cyclophyllum", a most mistrusted responsibility for the series.

Dr. Li, having perceived partially the difference in regard to the tube, has separated Sect. *Sigmantha* with the tube bent within the calyx from Sect. *Orthosiphonia* with the tube straight therein. Owing to the failure in tracing the origin of the structural peculiarity of *Sigmantha*, a manifest insufficiency of understanding has resulted.

As stated before, if the tube in the "Capitata-type" tends to bend, it is near the base and usually inside the calyx, *P. trichoglossa* Hk. f. (*vide* Text fig. I, C in page 82) and a few others being given for example.

Subsequently, we find in the alternate-leaved species *P. labradorica* Wirsing and *P. lapponica* L. and in the opposite-leaved species *P. floribunda* and *P. rigida* Franch. with their respective allies manifesting the same characteristic in the tube.

Dr. Li interprets with good reason the curvature of the tube as an inclination on the part of the plant to facilitate the landing of insect-visitors, and his view seems to agree perfectly with various steps taken by the plants in the evolution of this particular organ. If we put three species, *P. corymbosa* Prain, *P. comptoniaefolia* Franch. and *P. spicata* Pall. side by side, we shall at once notice the similarity in general habit on the one hand, and the three different degrees in the curvature of tube on the other. This fully supports my view in regarding *Verticillatae* not as a group of low status, but rather as one that has taken a line of development all to its own[1].

The general trend of evolution of galea as regards its length in contrast with the size of the lower lip is regressive, viz. the more advanced is the form, the shorter is its galea; this of course is only applicable to the vertical portion of the galea, as the horizontal part in the higher forms often prolongs into beaks. Thus all primitive species at the beginning of every group have long galea far surpassing the lower lip. In close coordination must this be with the spreading and enlarging of the lower lip in general and the curvature of tube in particular in group *Sigmantha*. If the curvature of tube is to be interpreted as a sign of advancement, then the *abbreviation* of galea must in all intention point to the same end, as a short galea would certainly make landing still easier for an insect than a long one that tops over the lower lip, and that is at least so in *Verticillatae*. Consequently, all short-hooded species of the series as *P. likiangensis* Franch., *P. holocalyx* H.-M., *P. spicata* Pall., etc. are in fact the climax forms in group *Sigmantha* instead of being the most archaic as they are generally considered to be[2].

Besides what is presented above, there are still other phenomena to be observed. These are as follows:

2. *Parallelism in evolution.*

One of the outstanding points of interest often encountered in the study of the genus is the phenomenon of parallel development in members belonging to different groups. The most perfect example in this respect pertains perhaps to two species, namely, *P. striata* Pall. (Pl. XXI, above) and *P. elata* Willd. (Pl. XXI, below). Superficially, the congeniality in their general habit, height, shape of leaves, even the length of the in-

1) Cf. observation under ser. *Verticillatae* by Dr. Li (Revision I, 300).

2) Cf. Dr. Li's arrangement of species in series *Microphyllae, Verticillatae, Melampyriflorae*, etc.

florescences soundly suggests their being close relatives; this is the reason why they are being kept together in the sect. *Apocladus* in Dr. Li's Revision. But an examination of the corolla at once reveals that they are not at all nearly related phylogenetically as the structures happen to belong to the two opponent "Basic corolla-types". The former, with a "Capitata-type" corolla is a member of group *Nothosceptrum*, while the latter with a corolla of "Flammea-type" truly belongs to group *Apocladus*. In progressing, the first evolves into *Proboscideae* and *Recurvae* while the second, with its near allies, *P. sudeticae* L. and *P. scopulorum* Gray develops into *Compactae, Incurvae and Surrectae*. A similar case of superficial resemblance is also found between species of ser. *Flammeae* and those of ser. *Capitatae*, especially *P. semibarbata* Gray, which is almost identical with *P. Oederi* Vahl and its allies in habit. There are, however, radical differences in the floral parts.

The monotypic ser. *Vagantes* (*vide* Pl. XIX, lower) which connects ser. *Acaules with Longipedes* by possessing both long-pedicellate basal flowers and axillary ones on long weak shoots is by no means an isolated case, for its near counterparts are found in ser. *Corydaloides* (*P. corydaloides* H.-M., Pl. XXII, above), which has more or less the same peculiarity. In spite of the fact that these two series are extremely similar in general features, so much so that they were kept together by Dr. Li in nearby groups, yet, what is seen in the order of anthesis in the two series makes their combination absolutely impractical, as the order of anthesis on the shoots of the former is centripetal, while that of the latter is decidedly centrifugal. It undoubtedly denotes a parallelism of development in two totally different lines of progress, as one is nearer "Capitata-type" as Group *Dolichomiscus* begins with ser. *Acaules* and the other is closely allied to the ser. *Flammeae* itself in both the order of anthesis and the shape of flowers.

Similar to the above are the cases between ser. *Acaules* and certain species of ser. *Longiflorae* like *P. decorissima* Diels and quite a number of others. Their superficial similarity must be regarded as due to parallel development rather than any real proximity in relationship.

The above cases of parallelism is seen in groups which bear but little relationship to each other, so such phenomena should be regarded as spontaneous coincidences without any phylogenetic significance at all. Another case of infinitely more interest is found between *Sceptrum* and *Cladomania*, two groups of very near affinity. Here the parallelism is exhibited in such an amazing manner that certain characters of one group are repeated precisely in the other. Such case is not to be regarded merely as one of common parallelism, but may be used to illustrate the similarity in developmental trends of closely allied groups, i. e. having sprung from the common stock and evolved definitely into separate lines of evolution, groups may still match each other in certain particulars

even to the finality of their turning points in evolution as in the present case.

In the subgroup *Eusceptrum*, ser. *Gloriosae* with one widely distributed species, the Eurasian *P. Sceptrum-carolinum* L. and all the remaining species in Japan have a green drying colour, and a broad-based lower lip. In the neighbouring series *Tristes* (sensu lat.) which, begins from Siberia down to China (incl. Tibet) and the Himalayas, a new starting point is marked by the nigrescent drying colour and strongly cuneate lower lip with comparatively narrower lobes as observed in many species like *P. Clarkei* Hk. f., *P. angustiloba* Tsoong, and *P. kongboensis* Tsoong etc. If we make a comparison of it with the group *Cladomania*, striking parallelism is manifested in the evolution of the two groups. The latter group, starting with Hirsutae-centripetae in the Arctic Circle, became widespread in Eurasia with *P. palustris* and *P. resupinata* L., and in North America with *P. lanceolata* Michx. There is little change in drying colour (except in *P. crenata* Benth. of the latter area which tends to become black), and in the shape of lower lip which as usual is rounded. But in entering southern China, the two characters mentioned above begin to make their appearance in the members of ser. *Carnosae* which is similarly a milestone of turning point in the group. The name of the first species of the series, *P. nigra* Vaniot (formerly of *Racemosae*, now transferred to *Carnosae*) is in itself sufficient proof for the nigrescent tendency of the plant, and a simultaneous consultation of the shape of the lower lip in the species of the series will not fail to show the identity in the second aspect.

3. *Retrogression and reversion of characters in evolution.*

It is fairly common to find retrogressive or negative steps within the normal or positive evolutionary scheme of plant-kingdom, and there is no exception in the present genus. As such, it is often manifested in the reversion of certain characters which have long been lost in the past through process of deviation in evolution.

Although of similar phenomena and facial value, the reversions seen in the present genus seem to be attributable to two categories which are of totally different nature. In some of them, the character or characters that recur are merely of an isolated and disjunctive nature that do not further influence the evolutionary trend; such reversion to lost characters should, therefore, be regarded as an arrested or static action. All such cases belong to the first category. In other cases, unlike the first, the recurring character or characters are not of a static nature, but may, on the contrary, denote a kind of evolutionary dynamism, as there usually tends to be marked rejuvenization of the group after the appearance of such a reversion.

Of the first category, there are several cases to be cited here.

We have fully discussed the improvement in phyllotaxy from alternate to verticillate by changing into opposite first. Thus from the opposite ser. *Salviaeflorae* (*vide* Pl. XVII, above), the subgroup *Eucyclocladus* developed in sequence of evolution into the verticillate *Melampyriflorae* (*P. floribunda* Franch., *vide* Pl. XVII, below), *Longicaules* (*P. Dielsiana* Bonati, Pl. XXIII, above), *Graciles* (*P. gracilis* Wall. subsp. *stricta* Tsoong, Pl. XXIII, below) and *Coniferae* (*P. conifera* Maxim., Pl. XXIV, above). Yet, at the farther end of the phylogenic line, there appears a form that has definitely opposite branches, leaves and flowers. This is *P. gracilis* Wall. subsp. *genuina* Tsoong[1], (Pl. XXIV, below). Its long, slender, somewhat flexuose and opposite branches, its leaf-shape etc. give it an aspect that at once recalls those of *P. salviaeflora* Franch.

In floral development, there is too, a solitary case in the partial reversion to primitive type, and that is found in a specimen of Soulié s.n. (1892). We know that the galea of *P. rhynchodonta* Franch. (*vide* text fig. II, C in page 83), to which this particular sheet belongs, has attained a medium stage in evolution wherein the short beak is furnished with a pair of main teeth with the addition of some much smaller, accessory ones. In this particular sheet, one of the flowers situated below the apex of the centrifugal inflorescence suddenly reverts to "Anodontae" type simulating those of *P. Oederi* Vahl.

The above cases are not only remarkable in nature, seeing how far distanced is ser. *Graciles* from *Salviaeflorae* and that "Anodontae" is spaced from "Rhynchodontae" by "Bidentatae"[2], but also very helpful to a systematist in revealing the intricate relationship between the present and the past.

For the second category, we may cite here a most instructive example. In the ser. *Palustres* of the group *Cladomania*, most species as *P. palustris* L. (*vide* pl. XII, below) and *P. sylvatica* L. have finely dissected leaves. After the turning point marked by *P. labradorica* Wirsing (Pl. XXV, above) which has deeply pinnatifid lower, but subentire, finely and shallowly double-serrate upper leaves, the character in the dissection of leaves becomes completely latent thereafter. Not until the group comes to ser. *Microphyllae* that this character is again manifested in *P. tenuisecta* Franch. (Pl. XXV, lower). A comparison of the general habit between this species and *P. palustris* L. would reveal that the lignification of the stem in the former is about the only vegetative difference from the latter. What is seen in *P. tenuisecta* Franch. really marks a new turning point of the group, as from this species have arisen a host of new forms that make the group still more prosperous.

---

1) Cf. observation under *P. gracilis* Wall. in the systematic treatment in Part II.

2) It should be noted that the "Bidentatae" comprises in reality two different stages of minor importance, i.e. the angulate form represented by *P. pseudoversicolor* H.-M. and the true bidentate form represented by *P. habachanensis* Bonati.

4. *Certain paradoxical phenomena in evolution and their possible explanations*

We have hitherto adduced only the sharp demarcation between the two "Basic types" as represented by *Rhizophyllum* and *Sceptrum*. If such a demarcation were to retain its sharpness uniformly throughout the genus, then the work of devicing a natural system would naturally become quite simple. But all evidences seem to indicate to the contrary. The sharpness of contrast decreases rapidly not only as the various groups ascend higher in the evolutionary scale, but also when the groups become less and less affiliated to the two representative groups. In addition to these, there even occur a number of cases wherein are found direct contradictions to the two "Basic corolla-types" as defined by us. To judge by the various phenomena exhibited, some of the perplexities seem to be attributable to the convergent nature of the general evolutionary trend; and as such, there are the following points:

1) The corolla—The general direction in the development of the galea is to lengthen its apex into a beak—a process common to both of the two "Basic types". In respect to the lower lip, it is obvious that the scheme for the "Capitata-type" is to gradually unfold from the erect, and to reach ultimately a horizontal position. The lengthening of the galea in both "Basic types" in combination to the spreading of the lower lip on the part of "Capitata-type" creates in the evolutionary line a middle realm, wherein the difference in corollal structures becomes rather obsolete. The difficulty in distinguishing the exact "type" is further enhanced by a similar state in the size of corolla, which, although being in reverse order one to the other in the two "Basic types", comes to meet at a particular level—the stage of *"Rhyncholophae"*—where they happen to cross each other. Herein lies the reason why the earlier authors failed short of clinging firmly to the "Basic types", which they recognized moderately critically in the lower realm, and began pooling all the species into the mixed "Rhyncholophae" when coming to this point.

2) Inflorescence—The respective order of anthesis, centrifugal for *Rhizophyllum* and centripetal for *Sceptrum*, is beyond doubt. Yet, the direction of progress is apparently unilateral, and is towards centripetal on the part of *Rhizophyllum*. Although in *Rhizophyllum* proper, the peculiar centrifugal inflorescence is carried into the highest development in ser. *Megalanthae* as seen in *P. elephantoides* Benth. and *P. bicornuta* Klotz. (*vide* Pl. VII, above and below), in the nearest subgroup *Rhizophylliastrum*, this character is already lost to a certain extent. Certain species as *P. yunnanensis* Franch., *P. rhinanthoides* Schrenk, *P. Franchetiana* Maxim. etc. are rather similar to some species of *Eurhizophyllum* on the same level of advancement except their often centripetal inflorescence. In the slightly farther away group *Apocladus*, the order of anthesis becomes completely centripetal, and there is no more difference in this respect from those groups nearer to "Capitata-type".

3) Habit—It is generally conceded that annuals are more advanced than perennials, and this seems to concur perfectly with what we see within the genus. This character too, seems to be the goal for the whole genus, although the level in its attainment is different regarding different groups. In the predominently perennial group *Rhizophyllum*, only some of the highest forms in the series *Pumilliones, Megalanthae*, etc. are annual or monocarpic in habit. In the opposite group *Sceptrum*, annual tendency is far earlier to appear and more prevalent. In the intermediate groups, those farther away from *Rhizophyllum* or nearer to *Sceptrum* are more marked in this respect. Thus group *Cladomania* is higher in the percentage of monocarpic species than all other alternate-leaved groups and comparatively, the verticillate-leaved groups are more favourable in this respect than the alternate-leaved ones. This point, too, contributes something more or less to the difficulty in finding an appropriate position for species in the higher levels.

The natural convergent tendency in development does furnish some answers to the puzzling phenomena observed within the genus, but it is not sufficient to cover all. It is especially inadequate to explain satisfactorily certain perplexities arising from contradictions against our definition of "Basic types" of corolla. To comprehend the nature of such phenomena, various cases must first be introduced in concrete forms. The main items of these are as follows:

1) Teeth of the galea—This is the most vexed problem which has very much puzzled the later authors. In all forms of tooth-growing, the most puzzling is duly the mysterious "Bidentatae". Bonati, after the formation of the two important points in his idea, namely, the lack of hybridization between "Bidentatae" and other groups, and the absence of dentate forms in ser. *Tristes* (sensu latissimo), assumed that the "Bidentatae" is an autonomous group, hence his system of 1918.

Dr. Li likewise seems to have experienced considerable difficulty in forming any definite idea as to which type of corolla is genotypically the most primitive, the "Anodontae" or the "Bidentatae". In our study, we have arrived at the definite conclusion, in partial agreement with Bonati's observation, that the galea of *Sceptrum* does not at all involve any dentate stage, while *Rhizophyllum* constitutes the typical tooth-growing group, although it too, begins with toothless forms. But Dr. Li's oscillation is by no means groundless, for there are cases of spontaneous appearance and disappearance of bidentate forms which are extremely difficult to get any satisfactory explanation. As an example, it is best to contrast *P. szetschuanica* Maxim.[1] to *P. rex* C. B. Clarke[2]. The former species be-

1) Var. *angulata* and var. *dentigera* are two varieties of *P. szetchuanica* Maxim. described by me in Dr. Harry Smith's collection of *Scrophulariaceae*.

2) Under *P. rex* C. B. Clarke var. *Rockii* (Bonati) Li, Dr. Li interprets strictly the teeth as the mucronate tips of the midribs of the original two corolla-lobes

longs to the series *Verticillatae* wherein the toothless forms are predominent and it is the only species of the series in which the angular and toothed forms suddenly make their appearance. The sudden occurrence of toothed forms in the toothless sphere seems to show that the teeth mean a recurrence of a character inherited but dormant. Reversely, in series *Reges*, all the normal forms of *P. rex* and its allies are toothed, and its var. *Rockii* Li is about the only case in which teeth are sometimes missing on the galea.

Again, in a number of cases, we see a typical "Capitata-type" of corolla being adorned with two teeth, as in *P. hirtella* Franch., *P. pteridifolia* Franch., *P. striata* Pall. etc. in the alternate-leaved groups, and *P. fragilis* Hk. f., *P. rex* C. B. Clarke, *P. melampyriflora*, *P. rigida* Franch. etc. in the opposite-leaved domain.

2) Lower lip—There too occur certain ambiguous conditions in regard to the position of the lower lip. Series *Palustres* as a unit is somewhat inconsistent in the shape of corolla. The flowers of *P. palustris* L. and *P. labradorica* Wirsing have lower lips in a rather erect position, almost identical with that of *P. lanceolata* Michx., a species having been kept in "tribe" *Personatae* by Steven. On the contrary, in their near relatives, *P. sylvatica* L. and *P. lusitanica* Link et Hoffm., the lower lips spread almost at a right angle—a fact not only noticeable in the dry specimens, but also observed personally in the field in the former species. Yet, the close affinity between these species is beyond question!

3) Length and curvature of tube—We learn from actual fact, as in the teeth of the galea, that in "Capitata-type" proper (the main line in grex *Sceptrum*), no species ever acquired a tube in any respectable length comparable to those of ser. *Longiflorae* and *Megalanthae* in the "Flammea-type"; in fact, the higher the form, the shorter the tube. Yet, in the group *Dolichomiscus* that started from ser. *Acaules* with the unmistakable stamp of trichome-bearing galea and the erect lower lip in the European *P. acaulis* Wulf, the highest forms in ser. *Muscicolae* compete favourably with their counterparts in group *Rhizophyllum* for the hegemony in tube-lengthening. This is in the alternate phyllotaxy. In the opposite, there are *P. cyathophylla* Franch. (*vide* Pl. XXVII, lower) and *P. flexuosa* Hk. f. var. *longituba* Tsoong of the group *Cyathophora* and

---

that unite to form the galea. Being, as stated, not a secondary growth, its presence is said to denote primitiveness. This is due to the abnormality in this particular case with a negative growth of teeth. This view is in a greater measure paradoxical to the opinion expressed in page 234; also contrary to the arrangement in his Sect. *Rhizophyllum* in which the dentate forms come after the toothless forms. As to the true origin of the teeth, it is very hard to be positive after a careful study. In my opinion, the teeth or auricles which sometimes appear at the anterior margin of the galea, thus forming the "Faucidentata-type", stand equally well for the position of the said tips as the teeth below the apex of the galea.

subgroup ***Asthenocaulus*** respectively, which also display tubes of considerable length, although their respective archaic forms *P. rex* C. B. Clarke (*vide* Pl. XXVI, above) and *P. fragilis* Prain have, discounting the presence of teeth on the hood, flowers after the true "Capitata" pattern.

The above listed examples well illustrate the intricacy of the problem. Unless we are prepared to take the facts as they are without making an inquiry into its cause, we must try to comprehend how such strange phenomena were brought about. For this, we have first to settle a question as to whether the evolution in the genus is divergent or convergent, that is to say, whether one of the intermediate groups had given rise to all the others which ultimately developed into the now sharply defined representative groups, *Rhizophyllum* and *Sceptrum*, or vice versa. Assumed it to be divergent, then it would become extremely difficult to try assigning any one of the intermediate groups like *Apocladus*, *Cladomania*, *Orthosiphonia*, *Sigmantha* etc. as the initiator of the genus, for there seem to exist always some objections both in morphological characters and geographical distribution which render such an assignment unsuitable. Reversely, all signs seem to indicate that the evolution is convergent, as morphologically most primitive species are concentrated on the respective initial end of the two representative groups with further testimony from the phytogeographical point of view[1].

When all present evidences point to a convergent evolution, there would be still less chance to have any vanquished forms which could have generated both these representative groups with floral and other accompanying characters so radically different, as the more primitive the form, the greater and sharper the differences.

If all possibilities of a monophyletic origin with divergent evolution are refuted by facts, then we are compelled to accept a postulation that the present genus is diphyletic, having probably arisen from two different species of a certain genus in some lower order.

In spite of the interspecific sterility barrier in most phenerogames, one still can not help presenting, upon the basis of a diphyletic origin, a hypothesis that in the early stage of development[2], being under more uniform environmental conditions, and in closer contact with each other within the Arctic Circle, hybridization took place between the species of the two opposing "Basic types", thus giving rise to less exact forms[3],

1) Cf. the discussion in the chapter of geographical distribution.

2) Here it is to be noted that by our judgement deduced from geographical distribution, group *Sceptrum* must have come into being much later than *Rhizophyllum*.

3) Through the cooperation of our colleague, Prof. F. H. Wang, I have examined the pollen grains of *P. Sceptrum-carolinum* L., *P. tristis* L. var. *macrantha* Maxim. and *P. Oederi* Vahl var. *heteroglossa* Prain, the first two leading species belonging to the "Capitata-type" and the third to the "Flammea-type". Not only is there great difference in the size of the pollen grains belonging to the

which later on, during alternating migrations, evolved under changed conditions into various intermediate groups, while the main lines of the two original types continued to progress down to present day as what we see in *Rhizophyllum* and *Sceptrum* respectively.

If the hypothesis be accepted, then all the problems raised above can be satisfactorily attributed to such a causation, for, paradoxical indeed are the phenomena to the "Basic types" of corolla; their occurences are by no means in complete chaos, but are found to be governed by certain regularities. In the question of bidentate forms, almost all intermediate groups are endorsed with toothed forms at certain stage of their develop-

---

two "Basic types", but they also differ very much structurally. Following are the descriptions of the pollen grains of the two species:

1. *P. Oederi* vahl var. *heteroglossa* Prain—Pollen grains oblate, 17.20 (16.92-18.33) × 20.30 (19.74-21.15) (the average of 20 grains). Grains 3-colpate, syncolpate. Exine smooth (Text fig. IV, A in page 98).
2. *P. tristis* L. var. *macrantha* Maxim.—Pollen grains oblate, spheroidal, 29.33 (26.79-32.43) × 31.56 (31.02-33.84) (average of 20 grains). Grains 3-colpate, not syncolpate, edge of colpus indistinct. Exine granular (Text fig. IV, B in page 98).

In G. Erdtman's "Pollen Morphology and Plant Taxonomy" (1952), the pollen grains of seven species of *Pedicularis* are diagnosed (pp. 403-404, fig. 232, B-D), namely, *P. Sceptrum-carolinum* L., *P. flammea* L., *P. Oederi* Vahl, *P. hirsuta* L., *P. rostrata* L., *P. palustris* L. and *P. sylvatica* L. Among these, *P. Sceptrum-carolinum* belonging to *Eusceptrum*, the representative subgroup for the "Capitata-type", has tricolpate pollen grains. *P. flammea* L. and *P. Oederi* Vahl, two species of *Eurhizophyllum*, the representative subgroup for the "Flammea-type", have also tricolpate pollen grains. The remaining four species, *P. hirsuta* L., still of the subgroup *Eurhizophyllum*, *P. rostrata* L. of the group *Apocladus*, and *P. palustris* L. and *P. sylvatica* L., the two members of group *Cladomania* have similar bicolpate pollen grains.

According to the theoretical evolution of pollen grain elaborated by A. L. Takhtajan (Тахтаджян, А. Л.: Морфологическая эволюция покрытосеменных Глава IX, рис. 80, 1948), there are two sources for the bicolpate pollen grains, one comprising those evolved from the monocolpate type, and the other the derivatives of tricolpate type. Now, in *Pedicularis*, the tricolpate pollen grains are found in the groups at the two extremities while the bicolpate ones are the products of the intermediate groups. Such circumstantial evidence gives further proof to my theory that the evolution of the genus can be nothing else than convergent.

It should be noted that *P. hirsuta* L., which retains a centrifugal inflorescence, also possesses bicolpate pollen grains. Although being kept in *Eurhizophyllum* on the criterion of its inflorescence, it may nevertheless be still of hybrid origin, with its opponent in *P. Lansdorffii* Fisch., a species having very similar habit but a centripetal inflorescence. This is a species which, in the evidences seen, is the progenitor of the species of ser. *Palustres*, a series with the juxtaposition of corollas in both "Basic types".

Prof. Wang has promised to carry out a series of examinations of the pollen grains of *Pedicularis* in 1956 to find out whether all the species of the intermediate groups and subgroups are furnished with bicolpate pollen grains. It is hoped that something worthwhile will be found out in the future.

ment, although the conditions of dentation are not all the same. Only those groups with prominent "Flammea-type" influence are beset with species furnished with a multidentate, "Rhynchodonta-type" of corolla, as *P. lutesescens* Franch., *P. lyrata* Prain of group *Brachyphyllum*, *P. gyroflexa* Vill., *P. mexicana* Zucc. etc. of group *Apocladus*. Furthermore, these forms, in conformation to the scheme of their own type, have also passed through the bidentate stage, for the former two species are the successors to the two-toothed *P. stenocorys* Franch., and the latter two are the descendents of the bidentate series *Comosae* and *Sudeticae*. On the other hand, those groups with predominent "Capitata-type" influence have corollas which involve no other stage than the single and simple "Bidentatae", as is seen in *P. hirtella* Franch., *P. striata* Pall., *P. pteridifolia* Franch., *P. rex* C. B. Clarke, *P. floribunda* Franch. and many others.

In respect to the size of flowers, the length of the tube and the position of the lower lip, we may take to the same view. The existence of the ambiguous position in the lower lips of *P. sylvatica* L. and *P. lusitanica* Link et Hoffm. side by side with the typical Capitata-typed *P. labradorica* Wirsing in ser. *Palastres* merely shows the hybrid nature of the series itself, and of the group *Cladomania* which has evolved doubtlessly from that series. So are the general sizes of flowers which, contrary to the scheme of "Capitata-type", become progressive in the group *Cyathophora*, being the smallest in the more primitive *P. rex* C. B. Clarke (Pl. XXVI, above), moderate in *P. cyathophylloides* Limpr. f. (Pl. XXVI, below) and *P. superba* Franch. (Pl. XXVII, above) and the largest in the most specialized *P. cyathophylla* Franch. (Pl. XXVII, below). This character, the long tube and the teeth on the galea combine to constitute the three controversial points in corolla of the general "Capitata" pattern which the group possesses.

As for actual instance of crossings, I have to acknowledge the inadequacy of my study in this respect. Nevertheless, I have the access to a number of hybrids cited by Bonati in his work. Owing to the fact that most of the later authors besides Bonati are reluctant in acknowledging the occurrence of hybridization in this genus, I would like to select for special illustration one hybrid mentioned by the French author, namely, *P. atrorubens* Schl. (Pl. XXVIII, below, and XXIX, above), of which there are ample materials for study. The parents of this hybrid are *P. recutita* L. (Pl. XXVIII, above) and *P. incarnata* Jacq. (Pl. XXIX, below), the former belonging to *Rhizophyllum* and the latter to *Apocladus*. The other points of difference are that the former has a centrifugal inflorescence and a corolla of the toothless type while the latter has the inflorescence centripetal and a galea rostrate. The hybrid comes in every respect between its parents, and is described by Bonati as follows:

"Diffère du *P. recutita* L. par son casque terminé par un bec court, mais très net, et du *P. incarnata* Jacq. par ses tiges glabres, son bec plus court, par la couleur de sa corolle, etc."

From the above, an omission of paramount importance has been made and this is the difference in the inflorescence. *P. recutita* L., like all true *Rhizophylli*, is endorsed with a marked centrifugal inflorescence which in *P. incarnata* Jacq. is decidedly in the reverse order. Not only this, the flowers in the former are closely set into a dense short spike, while those of the latter are rather loosely borne. In the hybrid, the inflorescence, like most other characters, is in an intermediate state. The order of anthesis can not be strictly said as centrifugal, as the flowers are brought into bloom almost simultaneously, and in respect to density, it is more often similar to *P. recutita* L. (*vide* Pl. XXIX, below), but the loose disposition after the fashion of *P. incarnata* Jacq. (*vide* Pl. XXIX, above) is by no means totally absent. This point certainly adds more weight to the inference of its being a hybrid.

Here is a case of hybridization not only between species of different groups, but also between corollas in different stages of advancement. It would be exceedingly interesting to find out how the populations of this hybrid are replenished in nature, whether by continuous crossing between individuals of the parent species or by the ripening of its own seeds, or by both. It will similarly be of profound interest to know whether there is hybridization between species at the two extremities of the lineal advancement, viz. the highest forms with the lowest, and also between those belonging to the two opposing "Basic corolla-types". As having been pointed out by several famous authors, hybridization has perhaps played a far more important rôle in the evolution of plant-kingdom than is generally acknowledged to be, and upon what we observed in the present investigation, we would certainly side with such opinions.

5. *Peloric flowers of Pedicularis.*

Peloric flowers are fascinating subjects in the botanical field, and it certainly would not be amiss to report a case here. *P. sylvatica* L. is a species with special inclination to produce peloric flowers. A case in the fusion of two terminal flowers of the inflorescence to form a dual flower is observed by Wigand and cited by Worsdell[1]. In this case, the flowers do not show any "regressive" phenomenon[2], for apart from the concrescence of different parts, the upper-lips of the two flowers are, though more or less modified, still in the shape of hoods (galea), and there is an additional triangular petal of unknown origin connecting the two lower lips.

There is another case of the same species in Kew Herbarium in which the upper lip is completely reduced into two separate normal corolla-lobes. The plant is a depauperate form, hardly 3 cm tall. There is no abnormality as far as leaves and calyx are concerned. There are but two flowers

1) Worsdell: Plant Teratology II (1916), 239; Pl. LI, fig. 6; text figs. 145, 146.
2) Vuillemin: Les Anomalles Vegetalis (1926), 106.

present and only one of them is in anthesis. The tube is about 18 mm long, at the apex of which spread the five almost equal, round-ovate limbs, those representing the hood being slightly smaller than those belonging to the lower lip. The interesting points of the phenomenon lie in the length of style and stamens and the number of the latter. The length of both organs seems not in the least affected by the reduction of the upper lip, for they are about 11 mm long, being approximately up to their length in normal flowers. Contrary to the length, the number of stamens is increased to five in correlation with the regression of corolla. The filaments protrude strictly from the throat of the tube and the upper part are pilose. The style is strongly deflexed to form a half-loop at about the middle of the exserted part, in corroboration with its original position in a normal flower. This is a case in which the phenomenon denotes unmistakably a sense of regression as differentiated from what is reported by Wigand.

6. *Remarks on general evolution.*

When one talks about evolution, one must have basis for his discussions to rely upon, and to a systematist, it has usually to be the criteria found in external morphology. Yet, the evaluation of such criteria is so speculative that those selected by one author may not only be inconsistent with, but even be contrary to, those picked out by another; moreover, the result does not necessarily corroborate with those obtained from experiments in other botanical fields. Upon such occasion, the assignment of systematic positions to various taxa, either primitive or advanced, will always be open to criticism and this is the greatest weakness in the inference drawn almost solely . from megamorphological criteria. Fortunately, unlike in any other genus, the congeniality in the vegetative characters in allied species in combination with the fixed orientation in the progress of the corollal structure has so lucidly demonstrated the lineal development in the present genus that there will be comparatively little chance to find reasons to doubt the systematic arrangement deduced therefrom. Thus, upon the basis founded on the evolution of the present genus, which forms an infinitisimal yet an integral part of the plant-kingdom, we may further demonstrate in some degree how, in general, the simple vegetation of the past evolved gradually through the long ages into an intricate profusion of to-day. Although here is scarcely a place to enter into the problem regarding the origin of species, and in spite of the fact that the present discussion has concerned itself completely to facial phenomena without inquesting into its causation, it is believed what has been observed in the present investigation may still be able to cast some light on certain particular phases in this delicate problem.

There are at present two different theories in connection with the origin of species: one is the older, Darwinian Theory and the other is the

new theory published by Lysenko in 1950. We are going to talk about certain points which would find proof in facts revealed in our study. By the old theory, species are formed through gradual and slow processes from varieties, which by stabilization and accumulation of slight variations, deviate farther and farther from their typical forms, and ultimately become new species; and because speciation is through such slow and gradual processes, there must exist, if not disrupted by extinction, transitional forms between the old and the new species. In this theory, intraspecific competition in the struggle for existence caused by over-population is regarded as the main stimulation through which new species are formed. By the new theory, species formation is materialized under a kind of interrupted progress by sudden, leaping processes; species are not derived from varieties which are but modes of existence of species; owing to the sudden nature in their appearance, there are evolutionary discontinuities between species; and between the old and the new, there are no linking forms at all.

Through our study in *Pedicularis,* it becomes quite evident that there are two totally different processes which contribute to the evolution of the genus. The first kind is by means of an even, step by step, process, and the second is by means of changes of a more radical nature which further happen in a leaping or "explosive" manner.

One particular phenomenon that draws my attention is the regularity with which the specialization in floral structures inside various groups and subgroups is carried on, *e. g.* from "Anodontae" through "Bidentatae", "Rhynchodontae" and "Longirostres" to "Siphonanthae" in group *Rhizophyllum.* Here is represented the first kind of progress, with its slow and even steps. In this kind of evolution, the changes in the floral organs not only are more eminent, but also, as a rule, precede those in the vegetative organs. This is, too, well illustrated by *Rhizophyllum,* wherein the latter see but little alteration from ser. *Flammeae* to *Macrorhynchae,* whereas the former have already evolved from "Anodontae" to "Longirostres" (*vide* Pls. IX, X, & XI, above). Similar conditions exist likewise in the whole lineal development of *Eucyclocladus* from *Salviaeflorae to Coniferae* (*vide* Pls. XVII, XXIII & XXIV), and in *Cyathophora* from *Reges* to *Cyathophyllae* (*P. rex* C. B. Clarke, Pl. XXVI, above; *P. cyathophylloides* Limpr. f., Pl. XXVI, below; *P. superba* Franch., Pl. XXVII, above; *P. cyathophylla* Franch. Pl. XXVII, below) respectively. Although in groups with a longer historical background, what minor variations in other respects accompanying the main changes in the floral structures would transform, in the long run, species on higher levels into very different forms, yet it is more than apparent that, if by such slow and regular process alone the genus were to progress, there would have come into being, besides the two initial groups, *Rhizophyllum* and *Sceptrum,* very few complementary ones, which are at present far more profuse and infinitely more complex in nature, to enrich the

Pedicularis flora of to-day. Such orthodox way of evolution will also go a very little way in accounting for the present state of infinite diversity and complexity of the plant life in our world. Some other means must have contributed something greatly to the function of evolution, and this is the second kind of progress alluded to above.

The abrupt, leaping processes peculiar to this kind of progress, though mostly displayed in a rather drastic manner, are usually singled out and made still more conspicuous by the strange effect of isolation through contrasting with the utmost regularity found in the successive developmental stages peculiar to the first kind of progress in the present genus. Here, radical changes may be manifested at one time in characters which are quite out of the scope of the existing species as the fusion of leaf-bases and bracts into cup-like gadget in group *Cyathophora* (*vide* Pl. XXVI, XXVII), and the sudden abbreviation or the apparent disappearance of the main stem in group *Dolichomiscus* (*vide* Pl. XIX), etc., or at another time in characters which had their prelusion in the old species which were, however, unable to establish them definitely, as in the change of phyllotaxy from alternate to opposite (verticillate). We have pointed out that there is great tendency in the genus for the alternate-leaved species to change into opposite—a phenomenon encountered in a great number of species, especially those of group *Cladomania* as *P. lanceolata* Michx., *P. palustris* L. (*vide* Pl. XII, below), *P. resupinata* L. (subsp. *oppositifolia* Tsoong), etc. Yet, however strong such a tendency is, not a single species in the alternate phyllotaxy has been able to gain and stabilize such a trait truly and decidedly. This shows that the appearance of groups with definite opposite phyllotaxy, though seemingly related to that tendency, is through independent and sudden processes; and by such kind of processes alone, more than half of the groups and subgroups in the genus have been accounted for.

Of course, if such abrupt changes, after stabilization, were to be left unsupported by the operation of the first or the orthodox way of progressing, which led the resultant forms to initiate their own respective independent lines of evolution, then these forms would only exist as some strange, isolated species for a certain length of period, and then die out without more ado in the tide of evolution. Supposed examples of such arrested action seem to be common-place; *P. hirtella* Franch., *P. tsekouensis* Bonati, *P. porriginosa* Tsoong may be named. So, it is the concerted efforts of these two different but inseparable kinds of processes that have put the wheel of evolution ceaselessly in action as we see it to-day.

In the slow progress of the first kind, phenomena in retrogression and reversion to old characters are very liable to occur, as in the sudden return of opposite leaves in *P. gracilis* Wall. subsp. *genuina* Tsoong within the long-established verticillate phyllotaxy of its more common form, the subsp. *stricta* (Wall.) Tsoong, and the unexpected reappear-

ance of an "Anodontous" flower in the inflorescence of the rudimentary-beaked, multidentate *P. rhynchodonta* Franch. Unlike in the first kind of progress, there will be no case in the reversion to old characters observable in the second, abrupt kind of processes.

From the above stated, a most interesting fact is revealed, namely, the co-existence of the radically different processes as asserted by Darwin and Lysenko in the evolution of plant-kingdom[1]. Not only they co-exist, but they actually cooperate closely to push on the function of evolution together. Darwin, with his voluminous knowledge in biological sciences, backed by his long series of experiments made under his meticulous observations, had taken the more prominent and more universal way of evolution, i. e. the first kind with its slow, gradual changes, as the sole means by which the organisms made their progress, but had apparently missed the second kind with sudden, "explosive" changes, which certainly occur far less frequently than the first kind, and are more difficult to discern, since any such case in the absence of intermediate forms can easily be attributed to a common causation of their having been exterminated in the competition with more perfect forms through the act of Natural Selection. But assuredly such explanation can not be applied universally to the evolution of organic beings, as it is rather doubtful whether there is any possibility in the existence of linking forms between the old species in the pre-existent groups and the new ones emerging through the second abrupt kind of processes. The new character or characters, as the connate leaf-bases and bracts which have so strongly characterized and isolated group *Cyathophora*, must have been acquired so suddenly that it is but natural that there are no intermediate forms to be left between the old and the new. And this is further testified by the absence of alternate-leaved forms of any opposite-leaved species.

That the reproductive organs of plants are more stable and less subject to vary than the vegetable parts is a fact generally known, and is also proved by results derived from experiments in anatomy, cytology, and other branches of botanical sciences more lately. Precisely against such general rule, the floral parts have manifested great plasticity in the present genus, while the vegetative parts appear to be far more stabilized and rather conservative in progress, as already proved by the examples in the two groups and one subgroup pointed out immediately above. The reason for such phenomenon does not seem to lie in that the present genus is constitutionally different from other phenerogames, but seems rather due to its peculiar entomophilous system of reproduction. To increase the efficiency in insect-pollination, the adaptation reflected in the changes of floral structures becomes extremely sensitive and eminent.

1) The process here referred to relates only to the superficial phenomena observed, but it does not necessarily mean that I agree with Lysenko's theory in the actual processes of species formation.

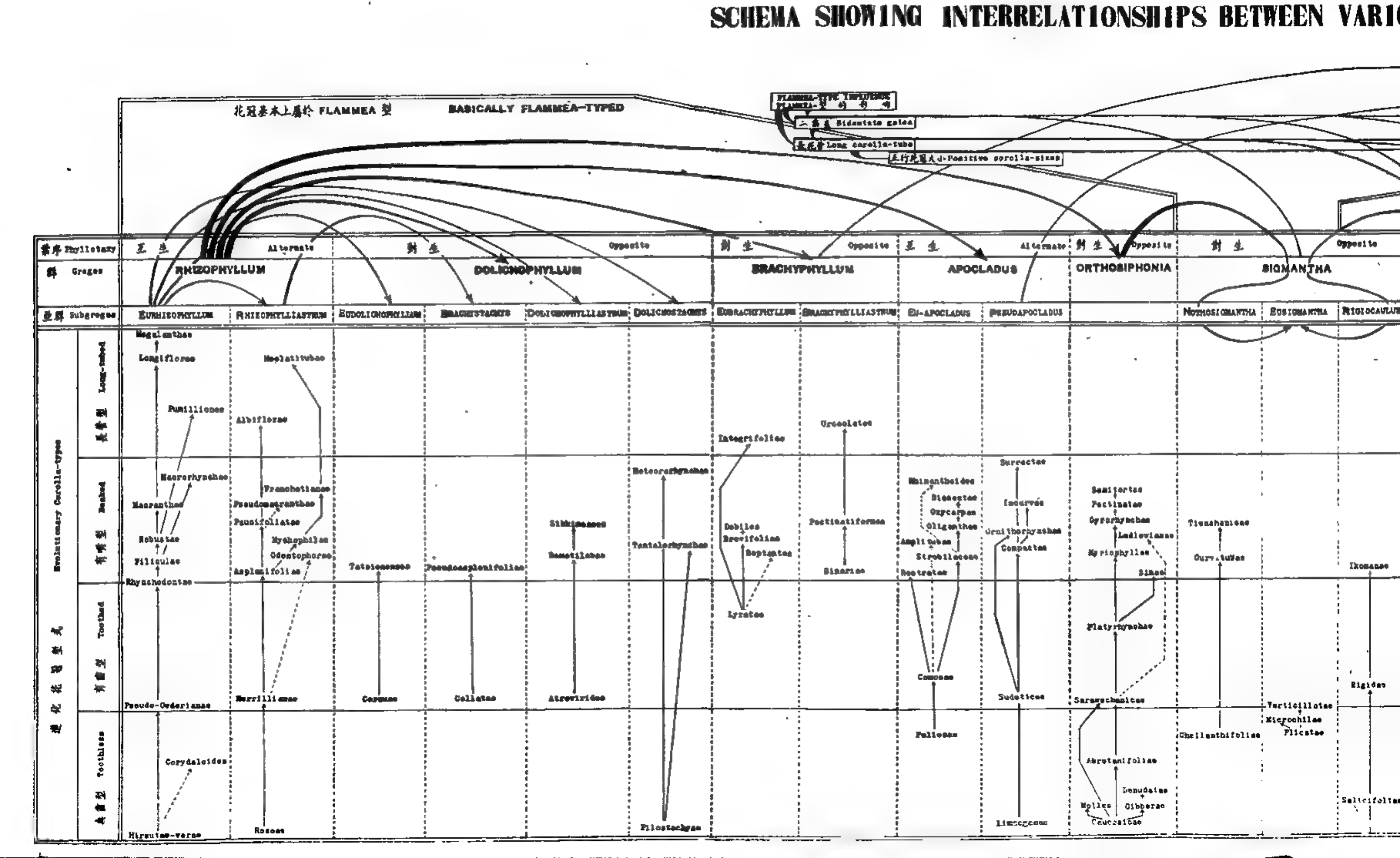
Here that the stimulation from the insect-pollination to the floral parts is far more intense and more direct than the influences from other environmental factors acting on the vegetative organs is almost beyond doubt. This shows essentially the importance of the rôle played by the environmental factors in the evolution of organisms, and how their multidimensional influences acting differently on organs of different systems have further intensified the diversity in variation. That the progressive changes in floral structure here are also contributory to the competition for existence induced by over-population as Darwinism, a partly Malthus-influenced theory, would have us to believe is a hypothesis scarcely acceptable to us.

On the other hand, upon the balance of evidence derived from the first kind of process with its fine gradations in differentiation, and its cases of partial reversions to characters long left behind—cases which indicate the intimacy and continuity in relationship between the old species and the new ones begotten through such procedures—one would be naturally inclined to disagree with Lysenko who has suggested that the second kind of process regulates exclusively the evolution of living things. His view-point with the assumption in the existence of sharp demarcation between species seems to be contrary to the experiences of systematists who are used to see, in their daily taxonomic works, more cases of slower progress with transitional links (varieties) between species than those of drastic progress having disruptive interspecific relationship.

(*To be continued*)

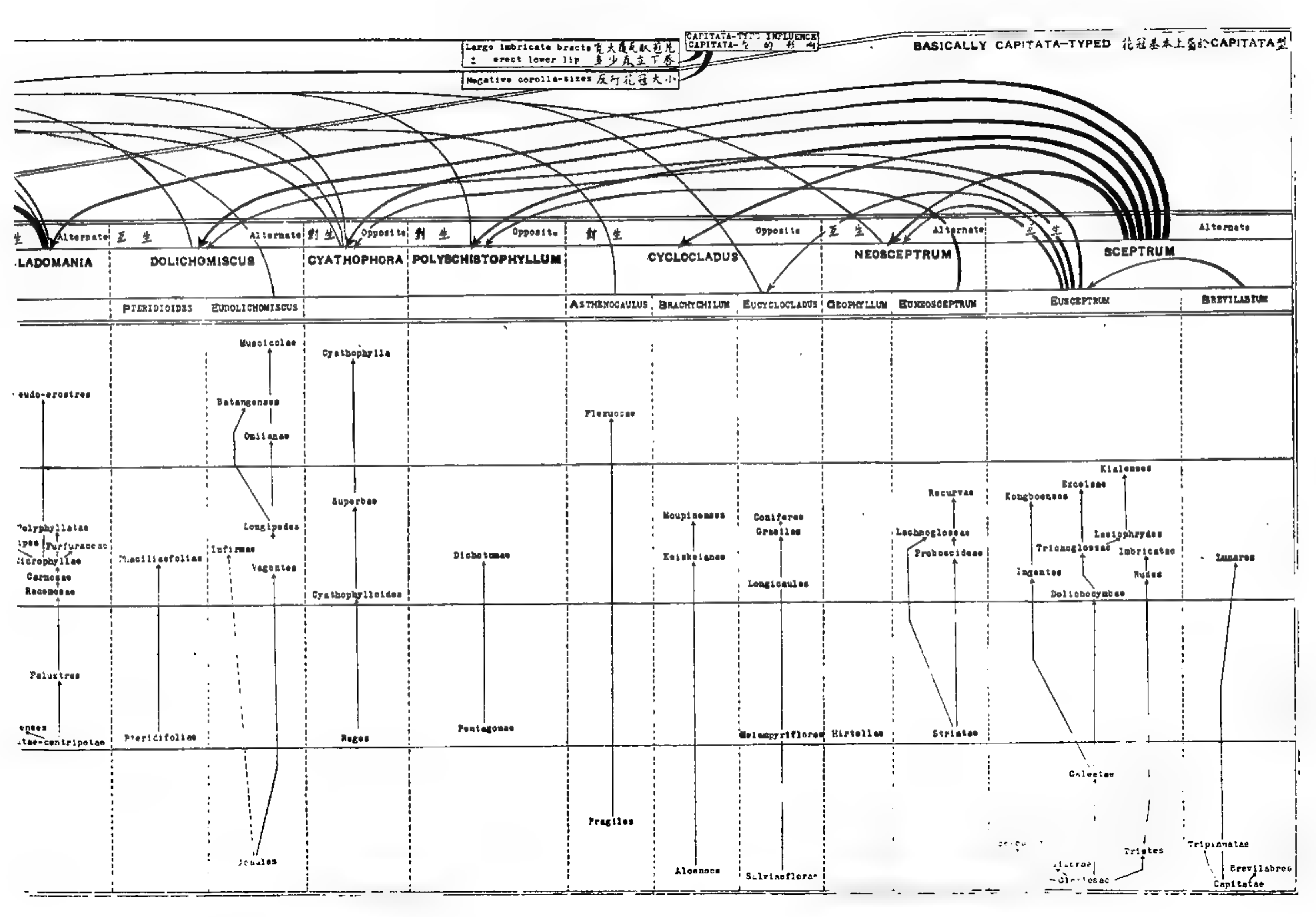
馬先蒿屬諸分類階層間相

SCHEMA SHOWING INTERRELATIONSHIPS BETWEEN VARIO



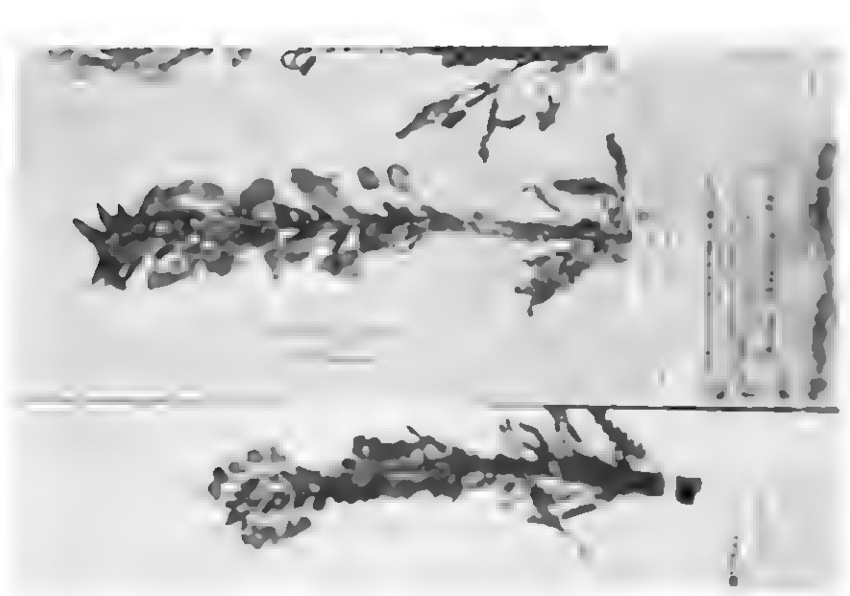
關係表解

S TAXA OF GENUS PEDICULARIS





P. dephantoides Benth.



P. bicornuta Klotz.



P. capitata Adams



P. oederi Vahl
subsp. *genuina* Tsoong
var. *heteroglossa* Prain



P. pseudoversicolor H.-M.



P. habachanensis Bonati





P. rhynchodonta Franch.



P. [illegible] Franch.



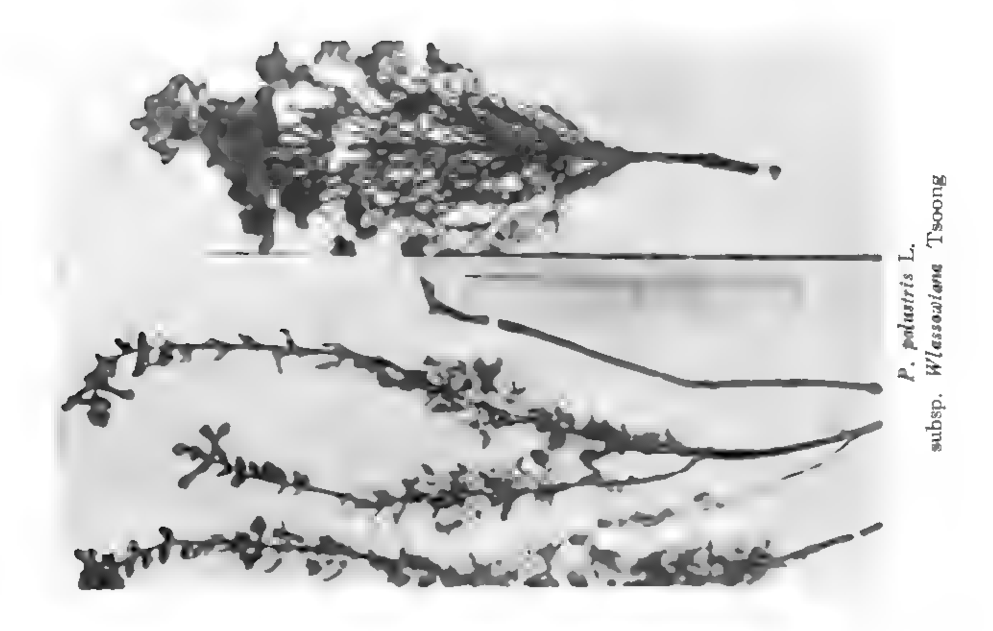
P. macrorhyncha Li



P. gloriosa Bisset et Moore



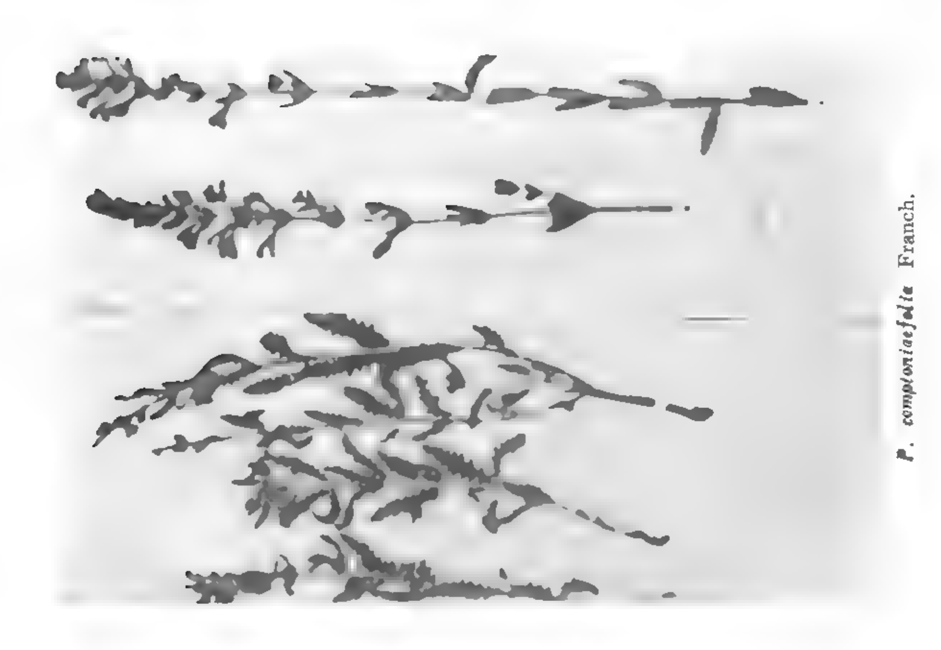
P. princeps Bur. et Fr.



P. palustris L.
subsp. *Wlassowiana* Tsoong



P. rigida Franch.



P. comptoniaefolia Franch.



P. corymbosa Prain



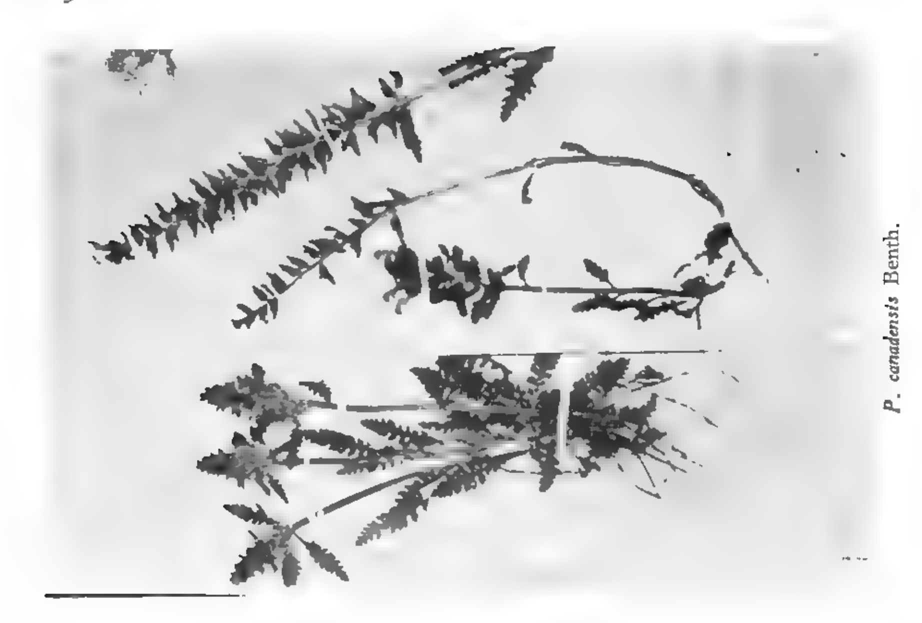
P. nigra Vant.



P. Mairei Bonati



P. verticillata L.
subsp. *latisecta* (Hulten) Tsoong



P. canadensis Benth.



P. cernua Bonati



P. salviæflora Franch.



P. floribunda Franch.



***P. Albertii* Regel**



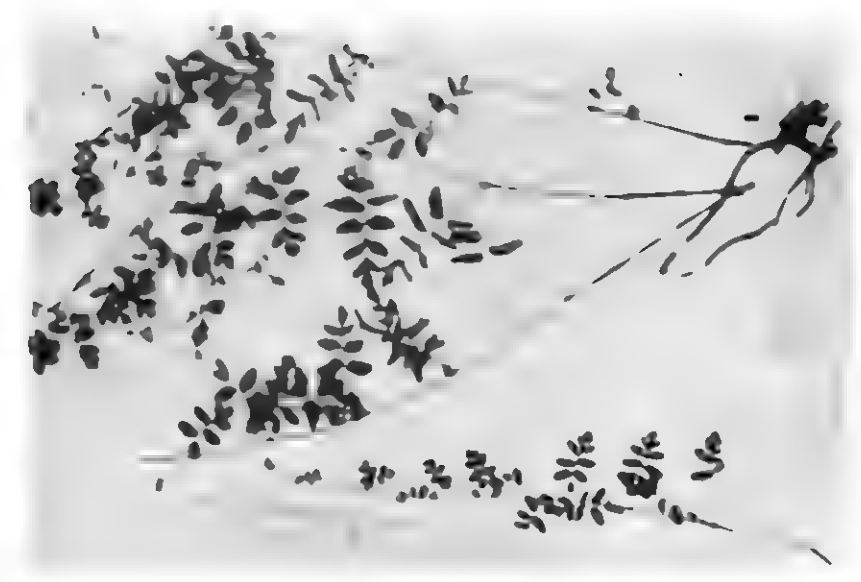
P. *pycnantha* Boiss.
subsp. *tenuisecta* (Lipski) Tsoong



P. acaulis Wulf.



P. vagans Franch.



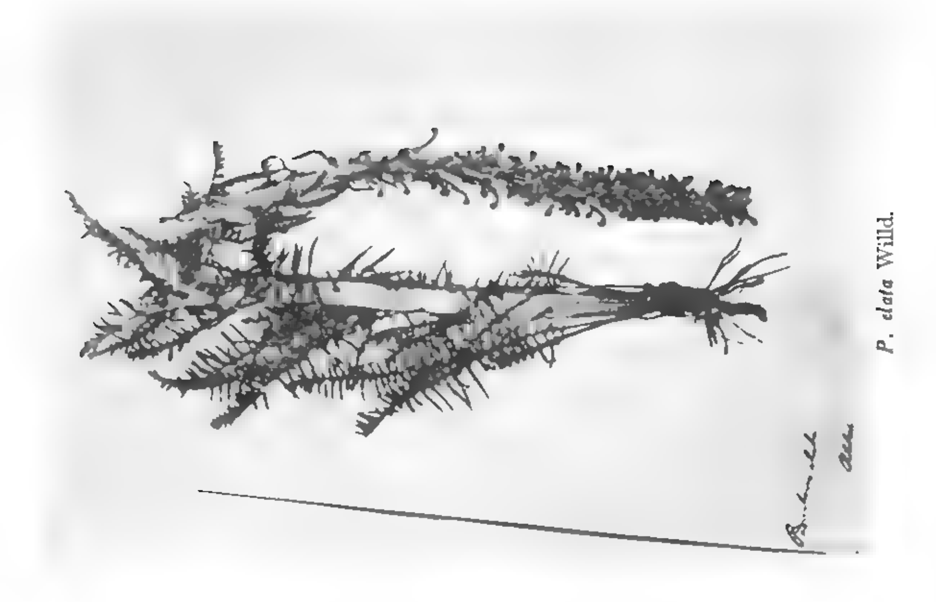
P. filicifolia Hemsl.



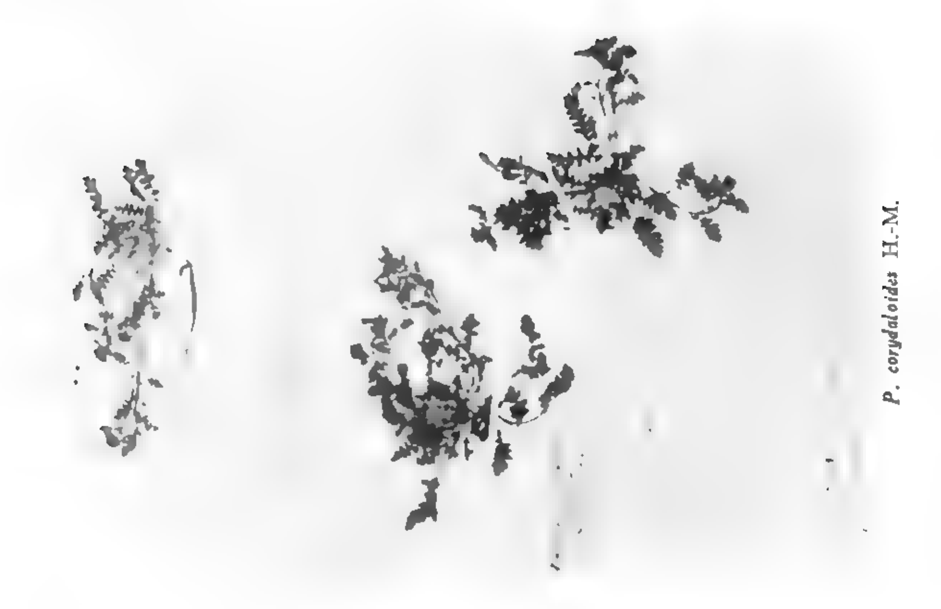
P. batangensis Bur. et Fr.



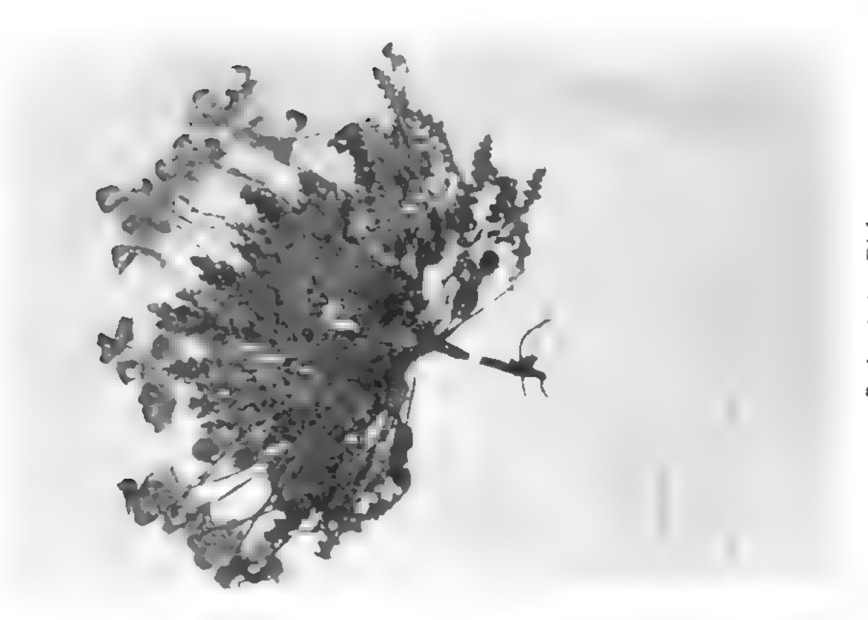
P. striata Pall.



P. elata Willd.



P. corydaloides H.-M.



P. dxorissima Diels



P. Diedsiana Bonati



P. gracilis wall.
subsp. *stricta* (Wall.) Tsoong



P. conifera Maxim.



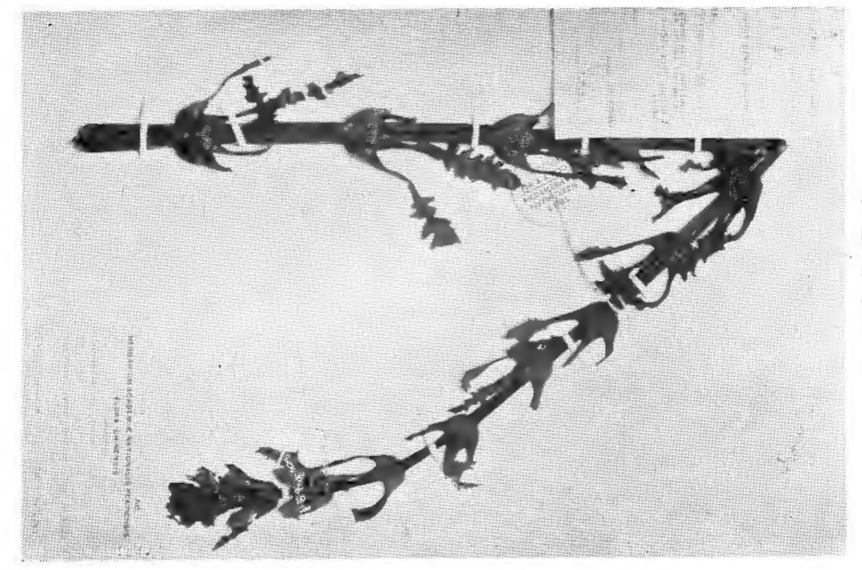
P. gracilis Wall.
subsp. *genuina* Tsoong



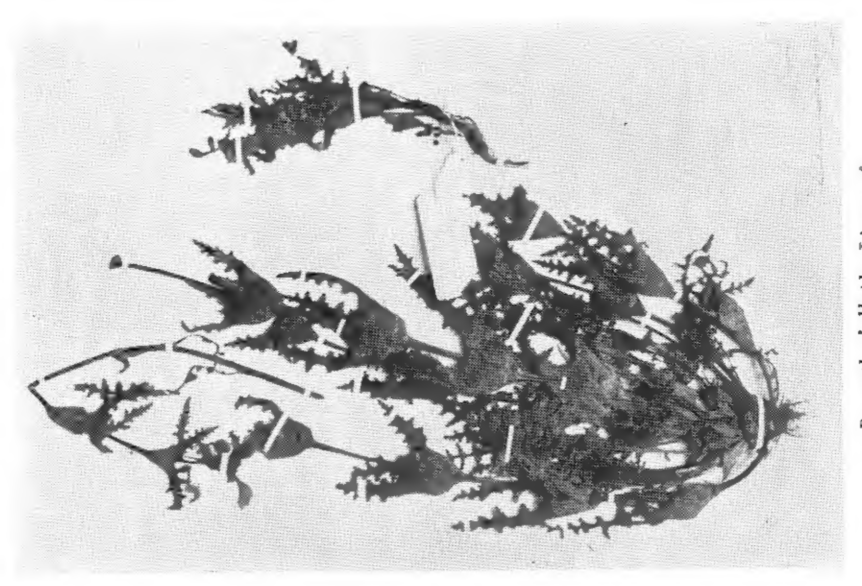
P. labradorica Wirsing



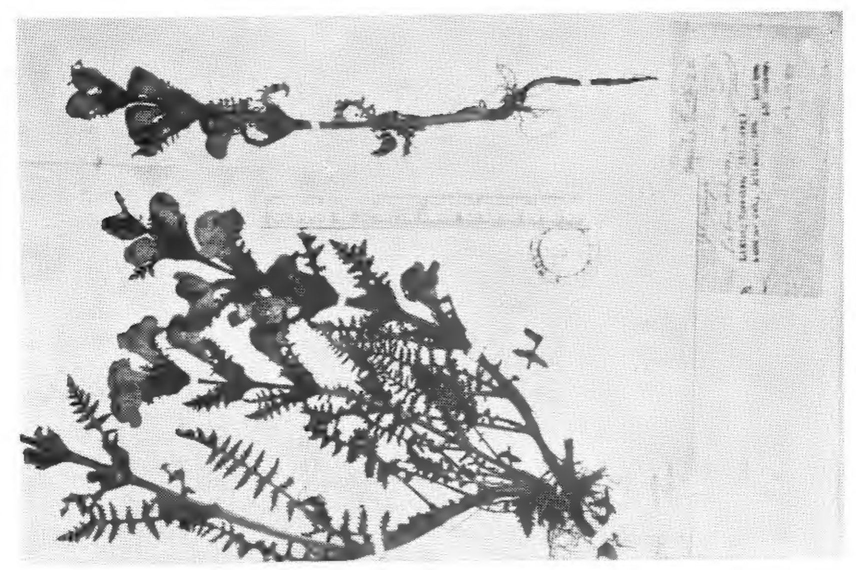
P. tenuisecta Franch



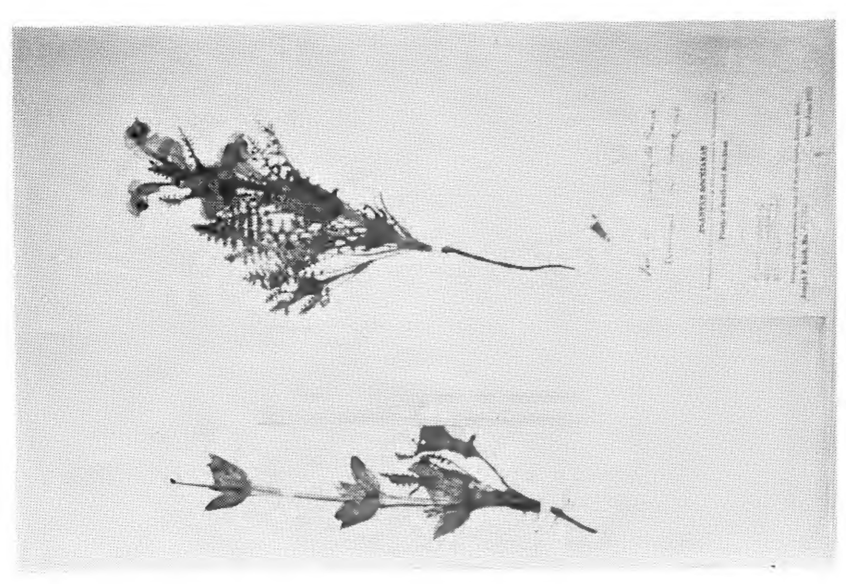
P. rex C. B. Clarke



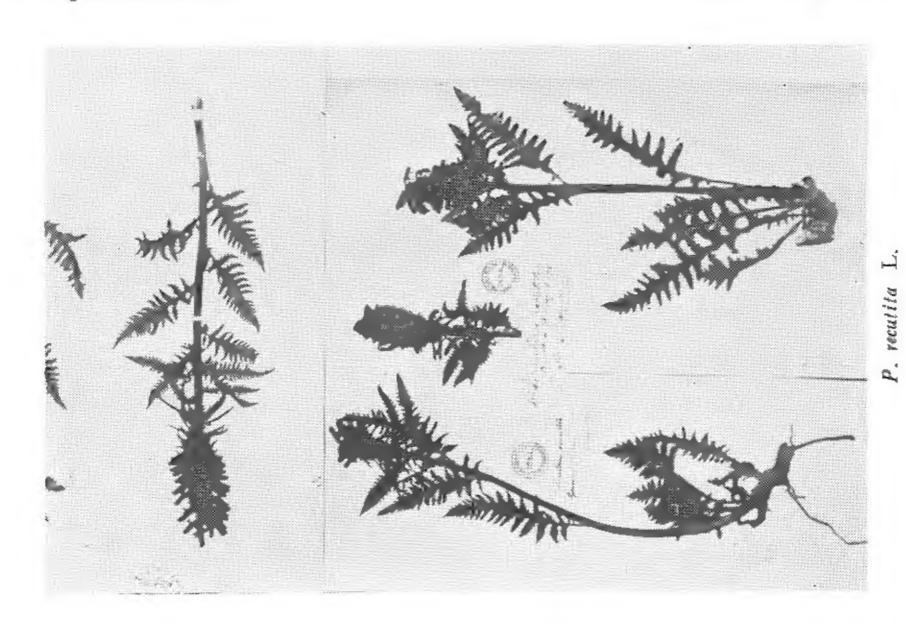
P. cyathophylloides Limpr. f.



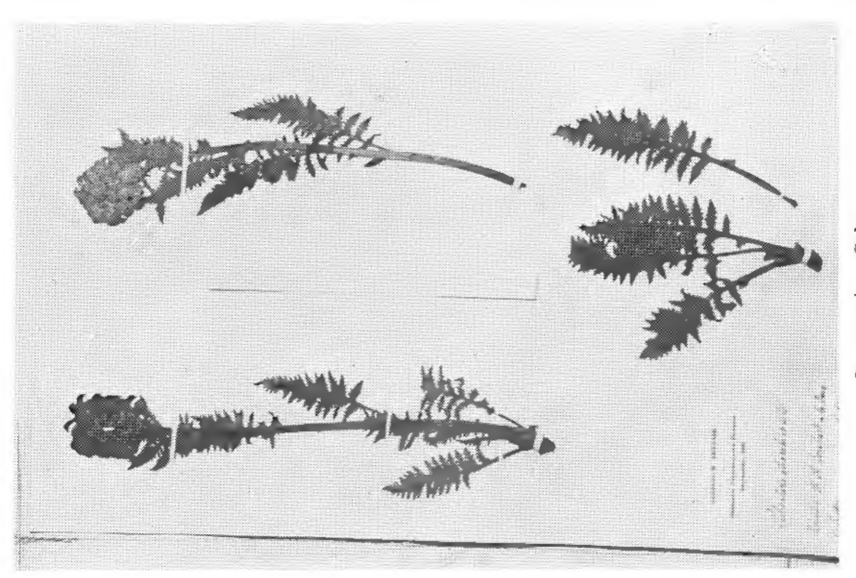
P. superba Franch.



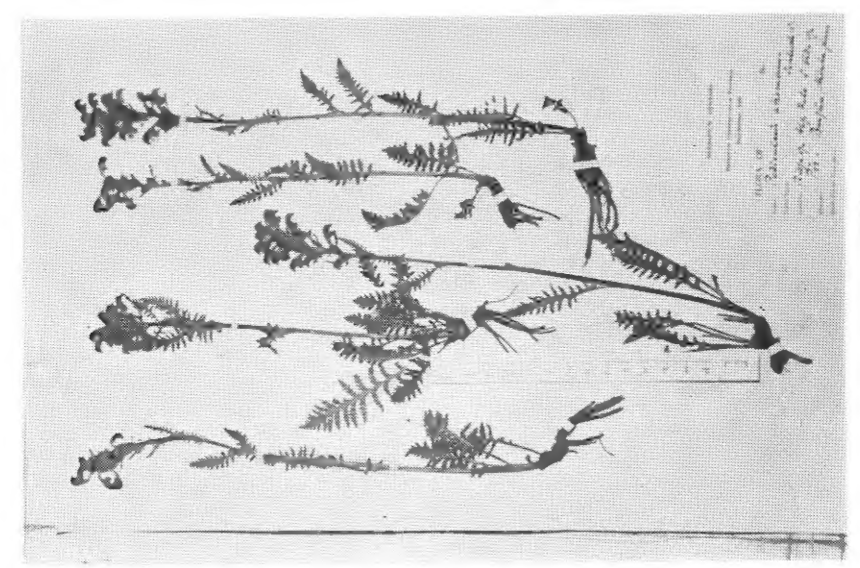
P. cyathophylla Franch.



P. recutita L.



P. atrorubens Sch.



P. atrorubens Schl.



P. incarnata Jacq.